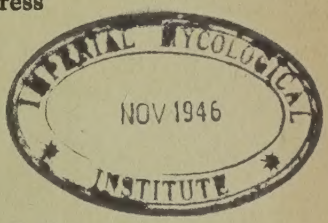
Vol. 12 No. 8

October, 1946

THE BOTANICAL REVIEW

Interpreting Botanical Progress



Fatuoid, Speltoid and Related Mutations of Oats and Wheat ..... C. Leonard Huskins 457

FUTURE CONTENTS
ON INSIDE BACK COVER

Published Monthly except August and September at
North Queen St. and McGovern Ave., Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
H. A. GLEASON AND E. H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
E. H. FULLING

Advisory Editors

PROF. S. A. CAIN, ecology
PROF. R. W. CHANEY, paleobotany
PROF. A. J. EAMES, morphology
DR. A. F. HILL, economic botany
PROF. JOHN S. KARLING, mycology
PROF. M. M. RHOADES, genetics
PROF. GILBERT SMITH, phycology
PROF. N. E. STEVENS, pathology
PROF. S. F. TRELEASE, physiology
PROF. CONWAY ZIRKLE, cytology

THE BOTANICAL REVIEW is published monthly except August and September. Subscription rate for the United States is $4.00 per year; for Canada and other foreign countries $4.25; single copies, 50¢. All subscriptions are payable in advance at par in Lancaster, Pa., or New York. Checks should be made payable to THE BOTANICAL REVIEW.

Manuscripts are prepared by contributing authors only upon invitation and on the suggestion or with the approval of the advisory editor in whose field the subject lies. Unsolicited manuscripts will not be considered. The editor, nevertheless, welcomes suggestions of topics which might properly be reviewed.

Missing numbers can not be supplied unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at N. Queen St. and McGovern Ave., Lancaster, Pa., or Fordham P. O., New York, N. Y.

THE BOTANICAL REVIEW

VOL. XII OCTOBER, 1946 No. 8

FATUOID, SPELTOID AND RELATED MUTATIONS OF OATS AND WHEAT

C. LEONARD HUSKINS

Dept. of Botany, University of Wisconsin

A. INTRODUCTION

Though the most commonly cultivated oat and wheat species are probably of considerable age (115, 142, 156) and both are commonly self-fertilized and therefore tend to exist as "pure lines", they continue to produce occasional off-type progeny. The most striking of these resemble wild or other related species. Darwin (36) and his contemporaries were interested in these off-types and "intermediate" forms for their bearing on the variation and evolution of cultivated plants. So also, towards the end of the 19th century, were many systematists. In the early years of this century geneticists were interested in them for their bearing on the problem of mutation and the origin of variations. When, in 1918, it was discovered that cultivated oats and wheat are polyploids with three times as many chromosomes as occur in the simplest species of *Avena* and *Triticum*, it became evident that an analysis of the nature and origin of the off-types would depend upon and contribute to an understanding of the special cytogenetics of naturally occurring polyploid species. Such an analysis is, of course, of practical value to the plant breeder as well as being of evolutionary and general cytogenetic interest. Further, the results have economic significance for seed growers and agriculturists in general, because the off-types are at best undesirable impurities in fields or in seed grain, and one of them, the "false wild oat" or Fatuoid, is often confused with real wild oats, which are a "noxious weed"[1].

Besides those off-type oats and wheat that resemble wild or other

[1] The reader interested in the mutational or cytogenetic aspects of the problem but not in the historical, evolutionary or purely agricultural ones is referred to Huskins (77).

related species there occur, of course, many others such as colour and chlorophyll mutations, and dwarfs, but these will be considered only incidentally in the present review.

Oats

Buckman (16) reported that "by cultivation and selection . . . *Avena fatua* has been made to assume the form of different varieties of cereal or cultivated oats", and further, that "the cultivated by degenerating may relapse into the wild state". In the light of present knowledge it seems probable that Buckman started his "improvement" work with natural hybrids between cultivated and wild oats, and, from his description, at least one of the "degenerating" forms appears to have been of the type which later became known as the false wild oat (33) or *fatuoid* (130). These resemble *A. fatua* in those awn and glume characters which are its chief diagnostic features, namely, that each grain of the spikelet has a twisted geniculate awn and an oval disarticulation surface, surrounded by dense pubescence (Fig. 1).

But in other respects, such as colour and shape of panicle, they are similar to the particular cultivated variety in which they occur. Almost invariably the fatuoids are segregates from heterozygous fatuoids, these latter really being the forms whose origin from normal cultivated oats has to be explained. The heterozygous fatuoids are more or less intermediate between the normal and the fatuoid in most of the characteristics which distinguish the latter forms. The heterozygous fatuoids have a twisted geniculate awn on only the primary grain of each spikelet. Secondary and tertiary grains of the spikelets are characteristically awnless. The base of the primary grains is nearer that of *A. sativa* than of *A. fatua,* and it is indistinguishable from the former on the upper grains. The fatuoids are readily recognized either in fields or in threshed oats, but heterozygous fatuoids often pass unnoticed. Fatuoids are, generally speaking, true breeding forms and hence are often called "homozygous fatuoids".

Forms intermediate between *A. fatua* L. and the cultivated *A. sativa* L. received much attention from systematists shortly after Buckman's time. A careful analysis of the differences between *A. fatua* and *A. sativa,* and of their relationship, was made by Haussknecht (62) in 1885. He found that these two species are linked by

a series of "transition forms" in which the "wild" characteristics of *A. fatua* are gradually lost: the oval disarticulation surface or

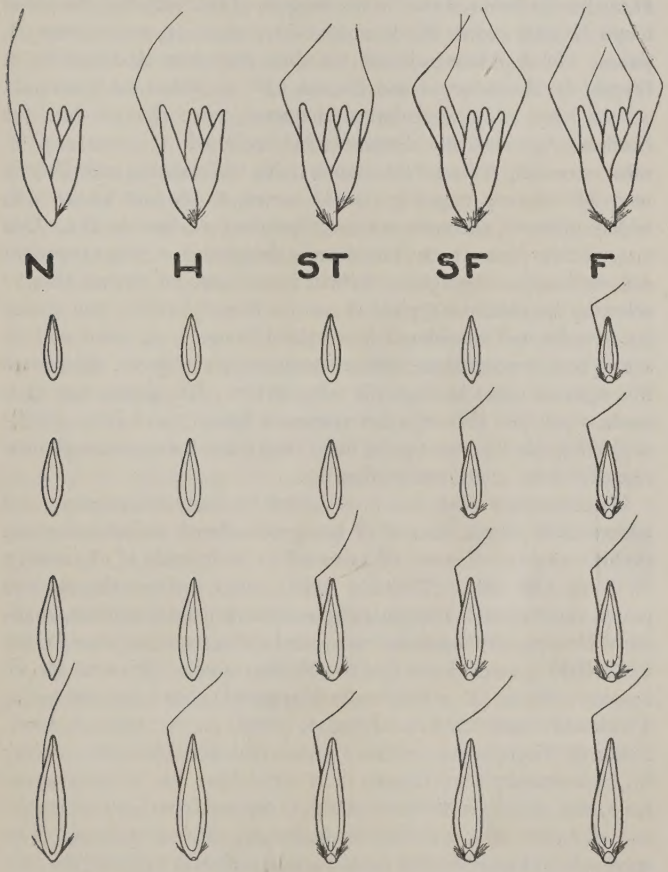


FIG. 1. Diagrammatic representation of the glume (hairiness and articulation) and awn characters differentiating normal (N), heterozygous mutant (H), steriloid (ST), subfatuoid (SF) and fatuoid (F) oat spikelets.

"sucker mouth" of the grains, which causes them to shed when ripe, is solidified step by step until disarticulation is possible only by

fracture, the pubescence on the back of the glumes disappears, and the awn either disappears or is reduced to a thin, weak structure. Haussknecht believed that in his analysis of this series of transition forms he had shown the gradual evolution of *A. sativa* from *A. fatua.* He therefore rejected the then prevalent classification of Durieu de Maisonneuve and Cosson (*27*) in which the Euavenae, on the basis of disarticulation character, were divided into the Sections Agrestes and Sativae; this assigned *A. fatua* and *A. sativa* to widely different taxonomic units, while within each Section were species only remotely related—some, as we now know, with widely different chromosome constitutions (see Section D). One intermediate form which Haussknecht designated *A. fatua transiens* was evidently a segregating hybrid form, since he reports that by selection he obtained typical *A. sativa* from it within four years. At first he had considered it a hybrid between *A. fatua* and *A. sativa* but, in accordance with contemporary standards, abandoned this opinion when he found it fully fertile. His description of it reads much like that of a heterozygous fatuoid, and Zade (213), neglecting the important point that it had a few hairs on the glumes, regarded it as such (see Section B).

Haussknecht's work was disregarded by many taxonomists, and intermediate forms, instead of being considered as indicating the evolutionary trend, were all assumed to be hybrids of *A. sativa* × *A. fatua* (10, 98). Thellung (175), who evolved the modern polyphyletic system now generally accepted for the Euavenae, vindicated Haussknecht's general views, and about the same time Trabut (182–184) gave evidence that the Mediterranean cultivated oat, *A. byzantina* Koch (*A. sterilis culta* Marquand), has been derived by a series of transition forms from *A. sterilis* L., not from *A. fatua.* Some of Trabut's intermediate forms had been described earlier by Haussknecht who, though he did not have the Mediterranean form, said that cultivated oats could be derived from both *A. sterilis* and *A. fatua.* The evolution of *Avena* and the interrelations of its species is still an unsettled problem, and it should be noted that the specific names used here are not necessarily those most acceptable to modern taxonomists, but those currently in most common use by agriculturists.

The intermediate or transition forms remained of purely evolutionary or taxonomic interest until the turn of the century when

oat breeders, especially in Europe and Canada, began to take note of the frequent occurrence of plants with wild oat characteristics in fields of cultivated oats. Experimental work on them was then started in several countries. Fischer (50, 51) observed that "wild oats" found in fields of cultivated winter oats differed in panicle shape from true *A. fatua*. In this respect they were always like the cultivated variety in which they occurred. He found, as have many others since (*e.g.*, 11, 55, 87), that they do not have the characteristic "delay germination" of *A. fatua* which enables its seeds to lie dormant in the ground over winter or for longer periods. He considered these forms to be spontaneously occurring "reversions" or "throwbacks" towards the original wild type.

In Canada during the period 1909–1912, several workers (26, 31–34, 43, 64) showed that false wild oats, or fatuoids, occur in many varieties of oats and are like the variety in which they occur except for the one group of diagnostic characters; that they tend to germinate immediately after falling to the ground and hence to be destroyed by cultivation or winter-killing, with the consequence that they are not a serious weed-pest as are real wild oats with their capacity for remaining dormant; and, correlatively, that they do not appear to increase in frequency in oat fields observed over a period of several years. Newman (121) and G. H. Clark (The Editor of Criddle's 1912 bulletin) added to these conclusions the fact established by Nilsson-Ehle (124, 125) that the group of characters comprising the "fatuoid complex" is inherited as a unit. Further evidence for these conclusions has since been presented (12, 19, 22, 116, 122, 163) and is again given in the more detailed genetical studies to be reviewed in Section B of this article.

Nilsson-Ehle (124, 125) records that Hjalmar Nilsson, his predecessor at the Plant Breeding Institution, Svalof, Sweden, had noted towards the end of the last century the important fact, already referred to, that the "atavists" or "reversions" which he found in many varieties and lines of oats arose from the normal in two steps. The first generation plants differed from those of the parental strain only in having a stronger awn and a more markedly pubescent base on the primary grain of each spikelet. These plants segregated in the next generation to give forms like themselves, the parental cultivated form, and fully formed "atavists" with hairy disarticulation-surfaces and strong geniculate awns on every grain

of the spikelets. These "atavists" were termed "fatuoids" by Nilsson-Ehle (130) who from extensive genetic experiments begun in 1900 concluded that they are "loss mutations", that cultivated oats have genes that mask or inhibit the effect of wild-type genes still carried in their genotype and that loss of these inhibitors permits the appearance of wild-type characteristics. Nilsson-Ehle's studies mark the beginning of the experimental work on fatuoids; they will be considered in Section B together with the work of his opponents, some of whom still uphold the theory that such fatuoids arise from natural crosses between *A. sativa* and *A. fatua.* In advance it may be said that much fruitless discussion would have been avoided if it had earlier been clearly realized that there are three classes of intermediate forms: *a*) those arising from natural crossing, *b*) the "heterozygous fatuoid" and other more or less similar forms now definitely known to be mutants, and *c*) the true-breeding "transition" forms of undetermined origin which provided the basis for the contention of systematists that *A. sativa* is derived by a progressive series of changes from *A. fatua.* These genetically diverse types sometimes cannot be distinguished without breeding tests, and some recorded tests made for this purpose have not been sufficiently comprehensive to give unequivocal results. Further confusion has arisen from the fact that while most workers, including the writer, use the term fatuoid as far as possible in the sense intended by Nilsson-Ehle who coined it, a few use it in its etymological sense to cover all fatua-like forms. The chief justification for the latter usage lies in the frequent indistinguishability of the fatua and fatuoid complex of grain characters when they are in the homozygous state. Nilsson-Ehle's usage involves consideration of other characters also. In practice it involves unanalyzed off-type plants being, at least provisionally, designated fatuoids if they appear to differ from the parental variety in only the one group or "complex" of characters, while those that differ in unassociated characteristics or otherwise give evidence of having arisen from crosses with *A. fatua* are termed fatua-like. The distinction, as will be shown, is difficult to maintain in some cases and may be impossible when both mutation and hybridization are involved, but without some distinction during analysis, only confusion results.

The speltoid complex of characters is distinguishable by experts from the analogous *T. spelta* complex, and less confusion has for this and other reasons arisen concerning wheat mutants.

Steriloids are mutant types that resemble the Mediterranean wild oat, *A. sterilis,* in their awn and glume complex of characters. They are found in varieties of both *A. sativa* and *A. byzantina.* Sub-

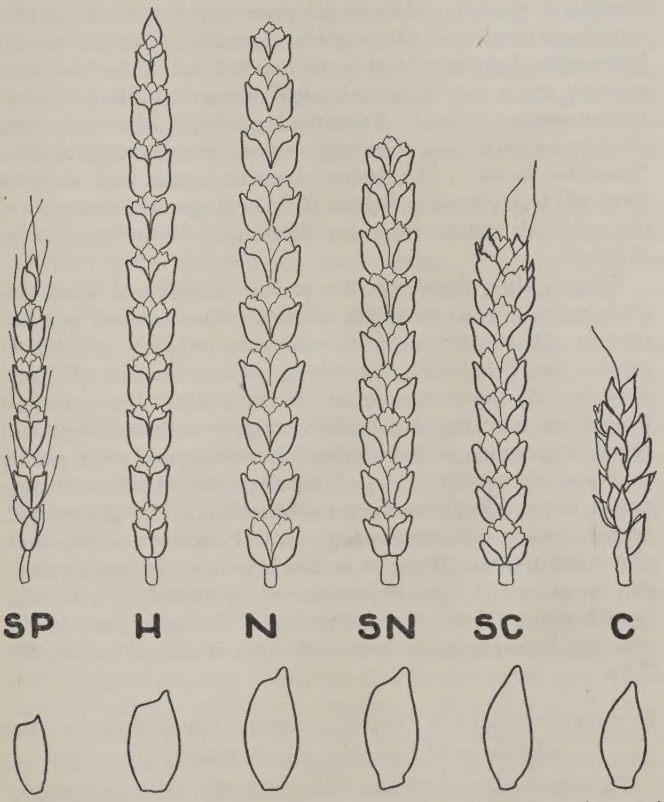


FIG. 2. Diagrammatic representation of the head shape, outer glume and awn characters differentiating speltoid (SP), heterozygous speltoid (H), normal (N), subnormal (SN), subcompactoid (SC), and compactoid (C) mutants of common wheat.

fatuoid and semi-steriloid forms also occur in both of these cultivated "species". Their diagnostic characters are illustrated diagrammatically in Figure 1.

Wheats

Nilsson-Ehle (127) reported that in 1904 he had found in a winter variety of *T. vulgare* Vill.[2] some plants more or less resembling *T. spelta* L., which he designated "speltoids". Later they were found in many varieties and in the progeny of intervarietal and interspecific hybrids. Most were bearded, but a few beardless speltoids and a few "compact-headed" forms resembling *T. compactum* were also found. From the beginning it was evident that these forms were characteristically mutants, not natural hybrids or "transition forms". The extensive genetic studies since made of them will be reviewed in Section C. The diagnostic characters of the principal mutant types are illustrated diagrammatically in Figure 2.

Winge (210) discovered that various off-types of wheat are characterized by irregularities of chromosome number and behaviour. He related their occurrence to the polyploid nature of *T. vulgare* (see Section D). Shortly afterwards Goulden (57) and Huskins (65) found more or less similar irregularities in various fatuoid oats and attempted to correlate them with the origin and genetic segregation of these forms. In recent years most genetic studies of *Avena* and *Triticum* have attempted to relate breeding data to the polyploid chromosome constitution of these genera, and, despite obvious differences, many parallel phenomena have been discovered in them. Hence in Section D some of the recent genetic data on wheat and oats will be reviewed together along with cytogenetic studies of both. General reviews of the speltoid and fatuoid problems have previously been made (47, 76, 78, 119, 138, 168, 205).

B. GENETIC STUDIES OF FATUOID, STERILOID AND SUBFATUOID OATS

The origin of Fatuoids—the Mutation Theory

The experiments of Nilsson-Ehle (124, 125, 129) showed conclusively that the heterozygous fatuoids he discovered arose through mutation and that the fatuoids were segregates from them. They were clearly not derived from natural crosses between *A. sativa* and *A. fatua*.

Many of them arose in pure-line varieties of *A. sativa* in an area

[2] *T. aestivum* L. under current International Rules of Botanical Nomenclature, but *T. vulgare* is the name almost universally used.

in which no *A. fatua* was known to occur. They resembled the variety in which they arose in all respects except the "fatuoid complex" of characters which in the "homozygous" form comprises a disarticulation callus or "sucker mouth" at the base of each grain of the spikelet, a tuft of hairs around this callus and on the rachilla, and a twisted, geniculate awn on each grain. This complex was found to behave as a unit in inheritance—crosses of true-breeding fatuoids with normal plants of the same variety gave an intermediate form which on selfing gave only normal, heterozygous fatuoid and fatuoid progeny, and these in ratios approximating 1:2:1.

The mutation was sometimes found to occur repeatedly in the same pure-line of oats. When it occurred in the descendants of crosses between different cultivated varieties, Nilsson-Ehle found the usual segregation for many characteristics differentiating the original parents, but the fatuoid complex of characters behaved as a unit in inheritance. Occasionally plants were found with the heterozygous fatuoid base type but awns on two grains of some spikelets, instead of the characteristic one on the primary grains only. This seemed at first to be a break-up of the complex, but Gante (53), one of Nilsson-Ehle's students, found it to be a non-hereditary fluctuation. Nilsson-Ehle (130) noted, however, that Surface (169, 170) had found some indications of a break-up of the fatua complex in crosses of *A. sativa* by *A. fatua*. Furthermore, in speltoid wheats which appeared to be analogous off-types he had himself (127, 128) found mutations affecting only one part of the glume-awn complex. Nilsson-Ehle concluded, therefore, that though the fatuoid complex behaved as a unit-character in inheritance, fatuoids probably differ from their parent variety by a "complex" of several closely, or even absolutely, linked factors or genes. They and speltoids were therefore termed "complex mutations". In 1920 he had speculated that mutations affecting a whole complex of genes might be "deficiency mutations" involving loss of a segment of chromosome like those then recently discovered, and interpreted as such from genetic evidence, by Bridges (14) in *Drosophila*.

Many authors have since confirmed Nilsson-Ehle's observations and supported the mutation theory of the origin of fatuoids (*e.g.*, 4, 7, 8, 23, 24, 40, 54, 65–84, 88, 89, 109, 118, 133–137, 149, 150, 167, 168).

Fatuoids almost invariably appear first in the heterozygous ("het") form, but Marquand (116) reported one case of a "homozygous" fatuoid arising directly from the normal. Alabouvette and Friedberg (8) had four cases and Oescu (139) one. It is naturally very difficult to rule out entirely the possibility of error, such as accidental admixture of seed, but Alabouvette and Friedberg feel sure that at least one of their cases is beyond doubt. In some varieties of oats fatuoids arise with a particularly high frequency. Fulghum, a variety classed as *A. byzantina,* is one such, and Coffman and Taylor (24) state that since het. fatuoids arise in it with the frequency of one in every 125 plants, the fatuoid might be expected to arise directly from the normal once in $(125)^2 = 15{,}625$ individuals. This would, of course, be expected only if the mutation occurred equally often in male and female gametes (or somatically), and if both male and female mutant gametes function as readily as normal ones. As will be shown later, the latter condition, at least, rarely occurs. The true expectation under ordinary conditions is, therefore, considerably lower than one in 15,625. Derick and Love (42) X-rayed seeds of the Trelle Dwarf oat which is probably a chromosome mutant (Derick, unpublished). The appearance of the plants resulting from these seeds was not recorded in detail but 3% of their progeny were fatuoids.

Fatuoids have now been found in almost all varieties and "species" of hexaploid *Avena* excepting *A. fatua,* in which they would be phenotypically indistinguishable even if the fatuoid complex were not genetically identical with the fatua complex, as it appears to be —apart from associated modifiers. They occur frequently in intervarietal and "interspecific" crosses. They have not, however, to the author's knowledge yet been reported in a completely awnless variety of *A. sativa* long grown in Central U.S.S.R. and latterly at the University of Alberta and elsewhere (see 68). The vigor and fertility of fatuoids approaches that of the parental strain when the chromosome constitution approaches the normal—as it does in most fatuoids that are picked up in ordinary seed selection work. Fatuoids picked out in special searches are often chromosome-deficient types of low fertility and vigor.

The Natural Crossing versus Mutation Argument

Nilsson-Ehle had emphasized the absence of *A. fatua* in the area where he found his fatuoids, and similarly Newman (122) recorded

that fatuoids occurred in Prince Edward Island where *A. fatua* was then unknown. Nilsson-Ehle also emphasized that fatuoids differ by several or many characteristics from *A. fatua:* Their lemmas are glabrous, not hairy, as in most forms of *A. fatua;* their panicle shape, grain shape and size and their germination are like those of the variety in which they arise; so, it may now be added, are other plant characters such as the ligules and the colour of the grains—with the partial exception of yellow (2, 89) which appears in some strains to be genetically linked to the fatuoid complex or its suppressor.

Nilsson-Ehle recognized, of course (125, 129), as did his supporters (*cf., e.g.,* 163 and the discussion following Crepin's 1927 report), that among the segregates of natural crosses between *A. sativa* and *A. fatua* there will appear types that are like fatuoids with respect to the "fatuoid complex" of characters. But, whereas fatuoids differ from the variety in which they occur only by this complex, which segregates as a unitary difference, the fatua-like segregates of natural crosses differ in and segregate for many other characteristics also. Thus natural crossing of cultivated oats with *A. fatua,* which is not uncommon and may occur over considerable distances (25, 41), will give rise to "wild" forms that may in some cases be distinguishable from fatuoids only by very careful examination and possibly only by breeding tests. In most cases, experienced workers, by taking note of other characters of the grain or the plant, can distinguish between them at sight, and Åkerman and Bader (7) stress that the structure and inclination of the base of the grains is alone sufficient to differentiate heterozygous fatuoids from the F_1 plants of any of their own *A. fatua* × *A. sativa* crosses, as the normal sativa factor is less dominant over the fatua gene complex than over the mutant locus.

Nevertheless, the uncomprising view that all "transition" or "wild" forms found in fields of cultivated oats are the result of natural crossing with *A. fatua* is held by several authors. Possibly this attitude stems in some cases from the disinclination of the older systematists to accept the mutation concept in general. It may now be encouraged amongst taxonomists by the close relationship assumed for *A. fatua* and *A. sativa* in the modern classification of the Euavenae, since this permits a wide range of fertile forms being considered segregates of common ancestry. Thellung, the

main author of the current polyphyletic system, supported Nilsson-Ehle in his earlier papers (175–177) but later reversed his views (178). Schultz (158), who is largely responsible for the polyphyletic system for wheat, believed Haussknecht's oat transition forms to be hybrids. Zade (211–213) collected especially vigorous intermediate forms with hairy glumes, which segregated cultivated, intermediate and wild types in a monofactorial, 1:2:1 ratio. The wild segregates had pubescent foliage-leaves and glumes. Zade considered them to be fatuoids, though they were clearly natural hybrids which did not fit Nilsson-Ehle's definition of fatuoids. Recently (see 7) Zade has become convinced that at least those fatuoids arising in established pure-lines of *A. sativa* cannot be due to natural crossing. Crépin (28–30) found natural hybrids between *A. sativa* and *A. fatua,* and from them, though they fulfilled the expectations set forth for such hybrids by Nilsson-Ehle, argued, with the support of Schribaux (157), against the origin of fatuoids by mutation. While Zade's and Crépin's observations were not on fatuoids and therefore do not give direct evidence on the origin of these forms, their studies and others (1) which will be detailed later, demonstrate clearly that fatua-like forms almost indistinguishable from mutant fatuoids may frequently be segregates from natural hybrids with *A. fatua.*

It is, however, difficult to appreciate von Tschermak's (185–191) prolonged attacks on the mutation theory of the origin of fatuoids. The weight of his position and authority has obviously influenced certain other workers, and there has been so much confusion of the issues involved that critical examination must here be given them. In so doing it will be necessary to emphasize and reiterate some of the elemental features of the problem. Tschermak reported that in the F_2 of *A. sativa* × *A. fatua,* there was an interacting two-factor segregation for the fatua-complex, this giving intermediates, sativa and fatua types in what he claimed as a 9:3:4 ratio (the actual numbers in the largest family were 444 intermediates, 132 sativa and 158 fatua). All other investigators of *A. sativa* × *A. fatua* crosses find a monofactorial, 1:2:1 ratio (1, 7, 8, 49, 54, 108, 110, 145, 169, 170, 214), though Florell (52) obtained a simple two-factor ratio of 12 byzantina: 3 sterilis: 1 fatua in the F_2 of *A. byzantina* var. Coastblack × *A. fatua.* A critical test of Tschermak's interpretation of his F_2 ratio is difficult because his F_3 material is

too limited. Åkerman and Bader (*7*), however, grew a large F_3, and while on Tschermak's interpretation two thirds of the F_2 sativa types should have segregated in F_3, all those they tested bred true, as expected on the monofactorial scheme. The intermediates all gave sativa, intermediate and fatua types in a 1:2:1 ratio, whereas on Tschermak's two-factor scheme only two thirds of them should have given fatua segregates in F_3 and the remainder should have either bred true or segregated only sativa and intermediate types. There is thus no evidence from their extensive data favouring Tschermak's interpretation. His results seem to be due to his method of distinguishing between F_2 sativa types and intermediates on the basis of the dorsal pubescence of the glumes—a rather unsatisfactory characteristic (see *7*, p. 15).

But Tschermak, extending his dubious interpretation of the *A. fatua* × *A. sativa* crosses to fatuoids (which he had not personally studied), argued further that they too are determined by the interaction of two independently inherited factors. If this were so, it would, of course, throw doubt on the mutation theory of their origin, since it would then be necessary to postulate that simultaneous mutation of two independent genes or gene complexes occurs not infrequently. Of his claim that the ratios obtained by various workers with het fatuoids were nearer to 9:3:4 than 1:2:1, it must be noted that he give no tests for significance, and that when Love (111) applied the χ^2 test to all the ratios cited by Tschermak it was clear that in only one case was his contention favoured. Actually there is nearly always a deficiency of fatuoid segregates and a corresponding excess of the sativa type (as was first shown long ago by Nilsson-Ehle), instead of the reverse expected on Tschermak's two-factor interpretation.

In its simplest form, as advocated by both Tschermak and Zade prior to 1918, the natural crossing theory of the origin of fatuoids ran into the insuperable difficulty, cited above, that whereas fatuoids are like the variety in which they arise except for the one complex of characters, the F_2 and later progeny of crosses between *A. sativa* and *A. fatua* segregate for or differ in many characteristics. To surmount this difficulty one would, as Nilsson-Ehle (130) remarked (translation), "be forced to the assumption, which cannot be called less than nonsensical, that white oat strains cross only with white *A. fatua,* yellow strains with yellow *A. fatua,* side-

headed with side-headed and so on". In their later papers Zade (213) and Tschermak (190, 191) attempt to get around this difficulty by making the assumption that the natural crosses which they postulate as the source of Nilsson-Ehle's glabrous white fatuoids must have been with yellow or grey glabrous *A. fatua* (white is rare; the commonest are black and hairy) and must have occurred many generations previously. By shifting the origin back to earlier generations, however, they only open up a new problem: the old pure-lines of oats in which some of Nilsson-Ehle's fatuoids occurred must now be assumed to be concealed heterozygotes, apparently breeding true to type, but actually continuing to segregate. There is no evidence for their having such a heterozygous constitution in the usual sense of the term and Tschermak offered no details. Heribert-Nilsson (63), however, put forward an ingenious scheme to explain not only fatuoids but recessive mutations, in general, as arising through segregation in concealed heterozygotes. Though invalid as formulated (see 130) Heribert-Nilsson's idea remains an historically interesting speculation, since we know now that being amphidiploids or allopolyploids, both *A. sativa* and *A. fatua* are probably of ancient hybrid ancestry. In a special sense, quite distinct from that envisaged by Tschermak, chromosome aberrations occurring in polyploids may be regarded as a kind of internal segregation or recombination process. This must not, however, be allowed to obscure the real issue in the natural crossing versus mutation controversy over the origin of fatuoids or other mutants.

By 1922 fatuoids had been found in a very large number of cultivated varieties of *A. sativa,* and the regularity with which they resembled the diverse parental varieties in characteristics other than those of the fatuoid complex led Garber (54), who favoured the mutation theory, to emphasize that on the natural-crossing theory of origin, it would be necessary to postulate some mechanism for the elimination of all phenotypes other than those which are like the parental strain, apart from the single complex of fatuoid characters.

Aamodt, Johnson and Manson (1) considered this elimination possibility in detail. They had crossed black, pubescent *A. fatua* with a white, completely awnless, glabrous *A. sativa* (Zhegalov's Selection 76) which, as mentioned, has the distinction of never having produced fatuoids (see 68). From four F_1 plants they had

grown an F_2 totalling 69 plants. These exhibited "practically all combinations between the parents in lemma-colour, awn development and pubescence" but only the three types of grain-base: fatua, intermediate and sativa. Fifty-four F_2 plants had black grains, eleven were grey and four were white. These white-grained plants comprised three with the intermediate base type and one with a fatua base. Their resemblance to heterozygous fatuoids and fatuoids, respectively, caused Aamodt *et al.* to call them "synthetic fatuoid types".

Coincidently these authors were studying "aberrant grain types found in threshed stocks and off-type plants selected in the field" from "elite" strains of Victory and Banner oats. Most or all of these appear to have been the products of natural crossing between *A. sativa* and *A. fatua*. Those that segregated produced populations "which corresponded more or less closely to certain types of segregation observed in the F_3 from the artificial cross".

Aamodt *et al.* were so impressed by this proof that many off-types which may commonly be classed as fatuoids are really the result of natural crosses, that they became "convinced that fatuoids arise through natural crossing between *A. fatua* and *A. sativa*", though they "admit the possibility of origin in other ways". From this standpoint they state that what "really needs to be explained is not the appearance of the fatuoid, but the more or less complete selective elimination of segregates other than fatuoids". "How is it", they ask, "that fatuoids are not found invariably in association with a host of black and grey off-types? The answer", they say, "is that fatuoids *have* been found with considerable regularity in association with these other aberrants. This is particularly true in fields grown from seed stocks which have not undergone selection for a considerable time". They recognized, however, that "in well-selected seed stocks, fatuoids are usually found unassociated with other off-types". To explain this they maintain that: "When selection is practiced in a field or plot, the black or grey segregates from a natural cross would be readily observed and removed, the homozygous fatuoid types would also be removed, but the heterozygous fatuoid type, similar in colour to the cultivated parent would, in many cases, escape notice and be propagated with the selected seed stocks".

Considering this suggestion, Åkerman and Bader (7) state

(translation): "Naturally it is possible that in this way heterozygotes may arise which in habit, etc., are very similar to the normal type. And this is especially the case when the original heterozygotes are backcrossed to the normal type".

To the writer it seems that the suggestion of Aamodt *et al.* contains both an under- and an over-statement: the heterozygous fatuoid when in plots of awnless varieties is not very likely to be missed by competent selectors and, on the other hand, it would require exceeding skill to pick out in a field all gray-seeded forms, all with pubescent grains, or all liguled segregates in eligulate varieties, *etc., etc.* Aamodt and his collaborators themselves had great difficulty in scoring their plants for gray or white grain, even in the laboratory. They conclude an account of their difficulties with the remark that "it is impractical to distinguish between white and grey grain colour". One asks, is it not probable that the difference between field and plot stocks is that in the latter natural hybrids with *A. fatua* are most likely to be picked out and eliminated at the F_1 stage, whereas in fields they may be missed at their inception and so give F_2 and later generation progeny that in some cases resemble the parental cultivated variety in many or most respects, apart from the fatua complex? Confusion of fatuoid-like hybrid segregates with true mutant fatuoids would therefore be much more likely to occur in field than in plot selection.

In any case it is unfortunate that Aamodt *et al.* did not emphasize that their "synthetic fatuoids" were classified as such only on three characters of the their grains—the fatuoid or het fatuoid base with white and glabrous lemmas. They were recombinants that on the basis of grain characters alone might well have been classified as fatuoids by any seed inspector of threshed grain who naturally would have no other basis of classification. Hence, the observations have great practical significance for seed growers and inspectors, especially in western Canada where *A. fatua* is a common weed and natural crossing with it takes place much more readily than in many other regions. The "synthetic fatuoids" were, however, definitely not fatuoids according to the generally accepted definition of the term. Seeds which Professor Aamodt and Dr. Johnson kindly supplied to the writer produced plants that differed from the parental variety of *A. sativa* in growth habit, pubescence of the foliage leaves, date of maturity and many other less definite char-

acteristics. This work is, then, very significant for the practical agricultural problem of the origin of off-types in cultivated oats, though not directly for the problem of the origin of true fatuoids. One may note, in stating this conclusion, that Åkerman and Bader (7), who examined several thousand F_2 and F_3 segregates of *A. sativa* × *A. fatua,* were unable to find any two identical with each other or with the parent variety when all plant characteristics were considered—this despite the fact that their crosses were with a glabrous *A. fatua.* Further, as Nilsson-Ehle originally pointed out and Åkerman and Bader have re-emphasized, the base of het fatuoid primary grains is characteristically very like that of the parental *A. sativa* strain, whereas heterozygotes of *A. sativa* × *A. fatua* have a more intermediate base-type. It seems, then, that fatuoids can often be distinguished from segregates of *A. sativa* × *A. fatua* by grain characters alone and can invariably be distinguished if all plant characters are considered. It should of course be borne in mind that the fatuoid mutation could occur in descendants of *A. sativa* × *A. fatua.* In that case the resultant true or mutant fatuoids, on account of their having some *A. fatua* plant characteristics, would probably be classed as natural hybrids. Error can invade from either side! In areas where natural crossing of cultivated oats with *A. fatua* is not infrequent, the combination of hybridization with mutation may produce complicated situations almost incapable of resolution. The complexity of the polyploid genetic and chromosomal constitution of *A. sativa* is, of course, directly related to its capacity to produce fatuoids by "loss mutation".

Recently, Taborda de Morais (171–174) has criticized the supporters of the mutation theory, particularly Alabouvette and Friedberg (8), and accused them of neglecting the possibility of natural crossing of *A. sativa* with glabrous wild oats such as *A. fatua* var. *glabrata* Peterson or var. *vilis* (Wallr.) Haussknecht. He claims that such crosses would result in F_1 plants phenotypically identical with *A. sativa* but segregating the wild parental type in F_2; these latter would then erroneously be called fatuoid mutations. Actually, Zhegalov (214), who has made these crosses, was well able to distinguish the F_1 of *A. sativa* × glabrous *A. fatua* from the *A. sativa* parent and also from het fatuoids by grain characters alone (see Figs. 54 and 55 in 115). The strength of the F_1 awn depends, like

that of het fatuoids (125), on the *A. sativa* parent, but even in crosses of the completely awnless variety Zhegalov's Selection 76 with *A. fatua,* awns distinguish the hybrid (1). Badly strained already, Taborda de Morais' hypothesis runs into seemingly insuperable difficulties when plant characters other than those usually considered important by taxonomists are taken into account, for example, only eligulate fatuoids arising in eligulate pure-lines of *A. sativa* (54, 89, 163). The decisive comment (130) quoted above, on the not less than non-sensical assumptions that have to be made to fit the simple formulation of the natural crossing theory to the origin of fatuoids, seems as appropriate here as to the earlier variants of the argument.

Chimeras or Mosaics

The most striking evidence against the natural crossing hypothesis for the origin of fatuoids is found in the occurrence of "chimeras" or "mosaics", *i.e.,* plants bearing both normal and fatuoid grains. The diagnostic features of fatuoids are glume characters composed, of course, of maternal tissue; the occurrence of two or more distinct types of grain on a single plant can not, therefore, be due to natural crossing. Chimeras must be due to mutation, using this term in its broader sense. The possibilities to be considered within the scope of this term are: (*a*) gene mutation, (*b*) chromosome aberration, (*c*) somatic segregation, and (*d*) various aspects, combinations or complications of these. Chromosome aberration may be considered a type of somatic segregation; chimeras may result from somatic crossing over in hybrids. But these, again, are distinct issues from those raised by the natural crossing hypothesis for the origin of fatuoids. Care must also be taken to see that supposed chimeras differing in entire culms are not really twin seedlings.

Tschermak (186–190) found one mosaic spikelet in the F_2 of an *A. sativa* × *A. fatua* cross. It had a brown, hairy, strongly awned fatua-type primary grain and a white, glabrous, weakly awned, sativa-type secondary grain. The fatua grain gave a fatua plant, and grains from neighboring sativa spikelets gave plants which (translation) "were all sativa forms and varied only in awning and hairiness of the base of the glumes". Similar mosaic spikelets were described by Tschermak in crosses involving different strains of *A. sativa.* It seems most likely that all his chimeras originated on

plants heterozygous for the fatua complex—a possibility which he admits but discounts. Chimeras in oat species hybrids have been found by others (*e.g.*, 15, 86, 148). Dr. H. Hunter (unpublished) analyzed a fatuoid-normal chimera found at Cambridge, and Huskins (70) described a complex one bearing normal, steriloid ("semi-fatuoid") and fatuoid grains. Another (80) bore fatuoid, sub-fatuoid and steriloid grains.

Diverse Ratio-types

The fatuoids discussed above are all of the type that gives a 1:2:1 ratio in F_2 when crossed with the normal type, and the het fatuoids from which they have arisen do the same when self-fertilized. For many years this "Series A" was the only ratio-type known, though three distinct ratio-types (roughly 1:2:1, 1:5:few and 1:1:few) designated "Series A, B and C" (128) had long been known in speltoid wheat. (These Series are here designated α, β, γ to avoid confusion with chromosome symbols—see Sections C and D). Amongst the het fatuoids from grains selected out of threshed samples of Banner oats by Goulden (57), however, was one that gave 20 normals, 15 het fatuoids and 5 fatuoids, of which two were dwarf. This is Series γ. Another het fatuoid gave 0 normals, 12 het fatuoids and 18 dwarf sterile fatuoids. This has now been designated "modified β Series" for reasons that will be given later. Nishiyama (133) obtained a strain of this type from a Series α strain supplied to him by the writer who has repeatedly found the same changed type in this strain. A het fatuoid plant found in a head-selection plot of Victory oats (69) gave seven normal, six het fatuoids and one sterile, dwarf fatuoid. In later generations involving many thousands of plants, het fatuoids of this strain have given these three types of progeny in ratios of about 1:30:1. They are classed as Series β, though the proportion of heterozygous progeny is much larger than in Nilsson-Ehle's Series β speltoids. A het fatuoid of the variety Kanota that gave nearly a 1:2:1 ratio, but with the fatuoid progeny dwarf and almost sterile (69), has since predominantly given normal and het fatuoids in more or less equal numbers and only a small proportion of dwarf fatuoids. It is Series γ, but sub-strains which must be classed as Series β continuously arise from it, as they do from Series γ het speltoid strains. Other variations of the basic α, β, γ Series ratio-types have also been found.

The ratio-types of fatuoids are at present more diversified than those of speltoids. But Series α remains by far the commonest type of fatuoid, whereas the three Series of speltoids apparently occur about equally often. It appears evident, however, that this is due more to the way the mutant forms are collected than to any difference in their frequency of occurrence. To get any idea of the frequency of origin the mutants must be discovered in the first generation, which is almost invariably the heterozygous form.

Het speltoids, being taller than their normal wheat sibs as well as distinctive in head-type, are easily noticed, while het fatuoids are not taller than normal oats and are not very easily picked out in the field. Fatuoids are much more easily noticed than het fatuoids, but speltoids not much more easily than het speltoids. When fatuoids or speltoids are picked out in a field they are usually of Series α because in Series β or γ the "homozygous" segregates are almost always dwarf and more or less sterile, and they usually fail to reach maturity when crowded.

There is another major difference affecting the frequency of the different Series in oats and wheat: fatuoids are very often picked out of threshed grain. Their progeny are then usually of Series α, since fatuoid seeds of Series β and γ are mostly sterile. Het fatuoids are rarely picked out of threshed samples of oats, for, while the primary grains of het fatuoid spikelets can usually be distinguished from normal grains, the secondary and tertiary grains can not. Speltoids and het speltoids alike are always picked up as plants or heads, since, being devoid of glumes when threshed, their grains can not be distinguished from normal ones. Further, speltoid or fatuoid strains originating in mosaic heads *i.e.,* by somatic mutation, are usually of Series β or γ, and mosaic heads of wheat are much more easily noticed than mosaic oat panicles.

It follows from the above that the fatuoid strains collected in the ordinary course of seed selection or improvement work are most likely to be of Series α, regardless of the frequency with which the different types originate, while for wheats the frequency of discovery, especially in well-rogued stocks, may be in some appreciable measure an indication of the relative frequency of occurrence of the mutations producing the different Series. On this latter point exceedingly little information is available for oats. Neglect of such considerations has led to several unfortunate controversies and misunderstandings.

Steriloids, Subfatuoids and Allied Off-types

Besides fatuoids there are off-types which in varying degrees resemble *A. fatua* or *A. sterilis* in basal articulation and awning. In *A. sativa* var. Sixty Day one off-type was found that "differed markedly from the normal fatuoid, in that its seeds were not dropped immediately on ripening and a decided tendency existed in many spikelets for the florets to remain together in threshing as is true with derivatives of *Avena sterilis*" (168). Huskins (70) obtained a strain of "semi-fatuoids", later called "steriloids", from one of a number of fatuoid-type grains found in a threshed sample of *A. sativa* var. Abundance. This steriloid type has "twisted and geniculate awns on both the first and second grains of each spikelet", but not on tertiary grains. "The primary grain has a medium-sized 'sucker-mouth', but the second has a solid base—like normal *A. sativa*". This off-type is, therefore, superficially like *A. sterilis* in awning and spikelet articulation, but the floret articulation is more like that of *A. sativa,* and in general plant habit and appearance it is typical *A. sativa* var. Abundance. Other more or less similar steriloids have been found in various varieties (19, 28, 29, 141, 145, 163). One in Kanota oats has been analyzed cytogenetically (80).

Jones (89) found a sub-fatuoid in an F_3 of *A. byzantina* × *A. sativa*. It has a fatuoid-like sucker-mouth on the primary grains, but the secondary and tertiary grains have only a partially developed disarticulation-surface and hence tend to remain attached. In some panicles the cleavage plane of the secondary grains was more rudimentary than in others, and there was "fracture of the rachilla at its base, as in *A. sterilis culta*" (*A. byzantina*). Pubescence of the sucker mouth and rachilla was like that of typical fatuoids. There were awns on all grains of the spikelets, but those of the fourth grain were very weak (personal communication from Dr. E. T. Jones—the fourth awn does not show in his published illustration). A "sub-fatuoid" found by the writer in the variety Kanota is very similar except that its fourth grains are awnless. (80). It may be significant that the variety Kanota has probably mixed *A. sativa* and *A. byzantina* ancestry.

Other off-types, too, have strongly developed awns associated with basal articulation nearer that of normal *A. sativa.* Many were found in *A. byzantina* var. Burt (21). Jones (89) described four distinct types from varieties of *A. sativa* or from hybrids of *A.*

sativa × *A. byzantina*. His and other analyses show that there is consistently a genetic association between base type, pubescence and awns, and it is indicated that many diverse forms behave as if they were members of a single allelomorphic series. It should perhaps be emphasized that no one has yet reported a hexaploid oat with fatua-type base but lacking awns. On the other hand, Jones (91) has shown that base and awn characters are independently inherited in diploid and tetraploid oats.

Amplifications of the Mutation Theory

In 1911 Nilsson-Ehle concluded that fatuoids arise through the loss of inhibiting factors which in normal *A. sativa* suppress the fatuoid factors that are always present in its genetic make-up. Jones (89) extended this interpretation to all the various off-types which, he showed, behave as if due to allelomorphs or a series of mutations on one chromosome. He considers the *fatua* or fatuoid to be the basic type and the cultivated form to be due to epistatic factors, on the "C" chromosome, which restrict the action of the primary awn and articulation genes. The mutations are changes of varying complexity which affect the epistatic factors, not the primary, wild-type genes. This concept is in general conformity with that adopted (69, 210) from cytogenetic evidence. It will be further developed in Section D.

Nilsson-Ehle had shown further that the degree to which fatuoid factors find expression in the heterozygote depends upon other independent factors (specific modifiers) present in the different cultivated progenitors. Many others (*e.g.*, 89, 145) have found modifying factors to be of very frequent occurrence and great significance in the expression of awn, pubescence and base type.

Some (7, 126, 149) have shown that the expression of the epistatic factors for the cultivated grain type is greatly affected by moisture and other environmental conditions, but that in the absence of these factors the hypostatic ("primary") fatua or fatuoid gene complexes are very stable in their expression.

Since Nilsson-Ehle's original mutation hypothesis for the origin of fatuoids is upheld by the evidence examined above, we may well conclude this section with a translation of the concluding paragraph of his 1921 (130) paper. This not only clarifies, and in the writer's opinion settles, all the older aspects of the problem, but em-

braces also the question still at issue—the nature of the mutation which produces fatuoids:

"The assumption must therefore be maintained that my fatuoids arise through mutation occurring in lines [of oats] which are homozygous in so far as the characters in question are concerned. As I stated in 1911, it is naturally not denied that fatuoid-like types can also arise through natural crossing with *A. fatua*. Indeed, cases are known where similar types can arise through either crossing or mutation. The fatuoids, segregating out of heterozygous fatuoids, that I have found in Sweden, are without exception mutations.

"Of course in saying this nothing is said about the cause or the nature and origin of the mutation. I, at least, do not imply in the concept of mutation anything but that through it a spontaneous hereditary alteration is produced which according to all the facts known to date has nothing to do with hybridization or segregation from hybrids. In what way, that is, by what change of the hereditary substance, the mutation arises is still an open question. If one speaks of the dropping out or loss of an hereditary factor every geneticist will understand that this is a purely formal expression which stresses the difference between the two members of a pair of allelomorphs and designates the alteration of A to a, but naturally does not say anything about the real internal process of change.

"But if anyone wishes in a wholly general way, and without considering the factual material against it, to ascribe mutations such as the ones described above to the consequence of hybridization, that is an inadmissable simplification of the situation which only obscures the problem and takes us further from a better understanding of it".

C. GENETIC STUDIES ON SPELTOID AND COMPACTOID WHEATS

Beginning in 1904, Nilsson-Ehle (127–129) studied speltoids from many varieties of *T. vulgare*. They arose as heterozygous forms and gave various segregation ratios. The first were found occurring in small numbers in a "square-head", dense-eared, variety and were distinguishable from it in the field by their longer, looser ears, longer stems or culms and later ripening. On mature heads the outer or empty glumes were shorter, almost square across the top, had stronger keels and bore green stripes running far down towards the base. Following self-fertilization the progeny of het

speltoids comprised about equal numbers of het speltoids and normal plants typical of the original variety. Crosses of het speltoids as female with the normal as the male parent gave a similar 1 : 1 ratio, while the reciprocal cross produced only normal progeny. Evidently, ovules bearing either normal or speltoid factors were produced and functioned equally often, but pollen bearing the speltoid complex was either not formed or did not function in this strain.

Het speltoids arising in other varieties differed less from their normal parental type. Some of them gave speltoid ("Sp") as well as normal ("N") and het speltoid ("H") progeny in ratios of about 3N : 5H : 1.5Sp. In these, speltoid-bearing pollen evidently functioned, though less frequently than normal pollen. In some strains the speltoid segregates were bearded and in others beardless. Other het speltoids were found later that gave only normal and het speltoid progeny in a ratio of about 1N : 5H.

The characteristics distinguishing het speltoids from normal *T. vulgare* are further accentuated in speltoids; their outer glumes are short, square across the top, very strongly keeled and highly indurated. When ripe they can not be bent away from the spike without breaking. The spikes are long and slender, *i.e.,* the spikelets are far apart.

The height and vigor of speltoid plants varies with the Series (see below) to which they belong. Vigorous speltoids are often confused with *T. spelta* and *vice versa,* but, as Nilsson-Ehle pointed out and Watkins (204) has since emphasized in detail, there are, usually at least, significant minor differences. The rachis of *T. spelta* is brittle and that of speltoids characteristically not. The keel of *T. spelta* glumes is gently curved, while that of speltoids is straighter and has a sharp "collar" at the junction with the rachis.

Classification of the Ratio-types

In 1920 the speltoids found by Nilsson-Ehle (128, 129) were classified into three series according to the type of segregation of their self-fertilized heterozygous form:

"Series A" het speltoids were those giving normals, het speltoids and speltoids in ratios ranging from almost 1 : 2 : 1 to nearly 1 : 1 : 0. The deviations from 1 : 2 : 1 were explained, after reciprocal crossing tests, as due to varying degrees of failure of speltoid-bearing

pollen to function in fertilization. This was confirmed by Åkerman (5) who found that in Series A the cross speltoid × het speltoid gave mainly het speltoid progeny (28H : 8Sp) and normal × het speltoid gave mainly normals (126N : 22H), while het speltoid × normal gave equal numbers (25 : 25) of het speltoid and normal progeny.

"Series B" het speltoids were defined as those giving a great excess of het speltoid yet few or no speltoid progeny (1N : 4 or 5H). Reciprocal crosses showed that their speltoid-bearing pollen almost never functions. They have also, Nilsson-Ehle shows, the additional complication that speltoid-bearing female gametes must be produced in great excess.

"Series C" het speltoids, on Nilsson-Ehle's original classification, produce slightly more normal than het speltoid progeny and very few or no speltoids. Non-functioning of speltoid-bearing pollen and the production of slightly more normal than speltoid-bearing ovules were held to account for this progeny ratio. Nilsson-Ehle had difficulty in deciding whether to assign some strains to Series A or to C, owing to the deviation of individual progenies. It is evident that zygotic elimination of het speltoids could play some part in determining the fluctuations and allow an excess of normals when plant mortality is high. In the studies of the writer and his associates all speltoids that give ratios close to 1N : 1H, with very few or no speltoids, are classed as Series γ, (α, β and γ being used in place of A, B and C, as with oats, to avoid confusion with chromosome symbols) and only those that produce an appreciable number of speltoid progeny of nearly or quite normal vigor are classed as Series α. This fits better the combined genetic and cytological data. It should, however, be stressed that there are intergrading types and that it now appears probable that the distinction between Series α and γ speltoids is one of degree only.

Nilsson-Ehle found that the degree to which the speltoid segregates differed in vigor from the normal was correlated with the degree of elimination of speltoid-bearing male gametes. Thus the relatively numerous speltoid segregates from Series α het speltoids are vigorous plants, the relatively rare ones from Series γ are weaker and the still rarer speltoids of Series β are weakest of all. Natural crossing, which is usually by normal pollen, occurs frequently in het speltoids which have weak speltoid progeny because

they are genetically unbalanced types and have much sterile pollen. It occurs rarely in those which have strong speltoid offspring because they produce abundant good pollen.

Series α, β and γ het speltoids can all originate directly from the normal, and by 1921 each had been found five times by Nilsson-Ehle. Series α usually remains constant in ratio-type, but as many as 12% of the het speltoid progeny of Series γ het speltoids have changed to Series β. Nilsson-Ehle (129) and Lindhard (105–107) obtained Series γ from Series β in a few cases, but the possibility of this being due to natural crossing by pollen of γ strains was not ruled out. Subcompactoids occur as rare but fairly regular segregates from Series β het speltoids.

In Nilsson-Ehle's het speltoids which arose in pure-line varieties the segregation was confined to one complex of characters; they could not therefore be the result of natural crosses with other varieties or species. They occurred repeatedly, though infrequently. In most respects speltoid mutants parallel closely the fatuoid mutants of oats. Just as the latter are similar to but not identical with *A. fatua,* so also speltoids do not conform completely to the type of *T. spelta.* Nilsson-Ehle classed speltoids, like fatuoids, as "complex mutations", *i.e.,* as mutations affecting an hereditary complex consisting of several genes, and here also he considered the possibility that they might be due to deficiency of a chromosome segment.

Vestergaard (201) found a Series γ het speltoid and noted that the flowers of plants which are sterile from either genetic or environmental causes may remain open for more than a week and that if they become fertilized it is usually by pollen from nearby normal plants. Lathouwers (99–102) analyzed the complicated segregation of several "speltoid-like" plants found in pure lines of *T. vulgare* and showed that they had arisen through natural crossing with *T. spelta.* Later (103) he found what he believed to be a true speltoid within a partly sterile progeny. It gave indications of having arisen through chromosome aberration. The "speltoids" found by Ducellier (44) were probably natural hybrids of *T. vulgare* and *T. spelta.*

Lindhard (105–107) studied in Denmark more than 100,000 descendants of a single het speltoid that appeared in 1914 in a squarehead variety of *T. vulgare.* The original het speltoid gave 18 normal ("squarehead"), 54 beardless het speltoid and two bearded

het speltoid progeny. Lindhard suggests that the bearded het speltoids may possibly have resulted from natural crossing; throughout his experiments bearded plants appeared sporadically. If the original plant was a Series β het speltoid it gave an unusually high proportion of normal progeny. In the light of later cases, it is here suggested that it was possibly a periclinal chimera, *i.e.*, one in which the outer cell layers were entirely het speltoid but the internal tissue, including some parts of the germinal layer, was in part composed of normal cells. With few exceptions the lines comprising the later generations of this family were Series β with the ratio of normal and het speltoid progeny ranging from 1 : 5 to 1 : 8. The normal plants were shown usually to be more viable than the het speltoids, and winter-killing, which was often very severe, apparently affected the ratios. Lindhard considered that a true ratio of 1 : 8 could, by zygotic elimination of het speltoids, be distorted to 1 : 5. In a few exceptional lines the normals were weaker than the het speltoids. One het "speltoid" that was obviously a natural hybrid gave a ratio of 1 : 12.

In the first four self-fertilized generations from the original het speltoid plant no speltoid progeny were obtained. In Series β the speltoid segregates are ordinarily very weak plants, and as mortality was very high in Lindhard's cultures they were probably eliminated either during the winter or at any rate before heading. In the fifth, sixth, seventh and eighth generations speltoid segregates were obtained in a few lines. Some of these were the dwarf, more or less sterile plants characteristic of Series β. Others were vigorous and fertile and were always associated with a marked change in the segregation ratio of their parent het speltoid. It now appears probable that natural crossing was concerned in their origin. They will later have to be considered further, as they were apparently the progenitors of the plants in which Winge (210) found most of the multivalent chromosome configurations on which he based his theory of the origin of speltoids. Throughout Lindhard's studies bearded het speltoids and beardless speltoids occurred sporadically. Some may have been new mutations, but others were probably due to natural crossing, which was apparently a serious complicating factor. Lindhard (105) recorded a "primary" speltoid mutation rate of 0.2%. In Japan Ichikawa (85) found 0.08% to 0.3% mutation from the normal type to speltoid.

Speltoids Arising from Hybrids

Kajanus (92–94) found that speltoids comprised 0.3% to 1.9% of the F_2 progeny of various intervarietal and interspecific hybrids. He concluded that they arise through some form of internal segregation. Leighty (104) found 1% to 3% in some intervarietal hybrids but none in others. Watkins (202–207) has analyzed in great detail the pentaploid hybrid *T. turgidum* × *T. vulgare* from which speltoid-like types are regularly segregated. His conclusion of present interest is that speltoids arise from pure *T. vulgare* by a process of internal segregation made possible by polyploidy. This was first suggested from cytological evidence by Winge (see Section D).

Chimeras or Mosaics

Åkerman (3, 6), Kajanus (93, 94) and others have analyzed vulgare-speltoid chimeras. Some of these are plants with distinct normal and het speltoid culms—the roots have to be examined very carefully to make sure that they are not really twin seedlings; even then the possibility presumably remains that fusion of tissues might have occurred. In others a single head bears both normal and het speltoid spikelets, the line of differentiation usually being lateral. The diagnostic characters, being in maternal tissue, give no indication of the genotype of the grains borne on these heads. Sometimes grains from both parts of a chimera produce only normal offspring. Evidently in these cases the epidermal tissue but not the germinal layer has been affected by somatic mutation. In other cases the grains from normal sectors produce only normal plants and those from het speltoid sectors give both normals and het speltoids, showing them to be germinally het speltoids also. A speltoid developed from a seed produced in a het speltoid sector on one of Åkerman's chimeras. Het speltoid plants developing from the grains of a chimera often belong to Series β, but the immediate progeny-ratio of a chimera is naturally not significant for determining the Series, as it depends entirely upon the extent to which the mutation affects the different tissues of the parent plant. Lindhard (105) and Ishikawa (85) found "het speltoid-subcompactoid" chimeras in *T. vulgare,* and Nilsson-Leissner (132) found "spelta-vulgare" chimeras in the progenies of crosses between *T. vulgare* and *T. spelta.* Nilsson-Leissner's chimeras were usually heterozygous spelta with

a vulgare epidermal sector. We may smile at 17th and 18th Century reports of mosaic wheat heads bearing oat spikelets (see 215) but one can not help wondering how men like Gerard, Cooke and their contemporaries came to give such particular accounts of them. Could the "oat" spikelets have been somatic mutations to a *T. polonicum* type of glume, perhaps from *T. turgidum* which, like *T. polonicum,* is a tetraploid species? *T. turgidum* has long been widely grown in England, and *T. polonicum* type glumes occurring sporadically on heads of it could have been mistaken for oat glumes if this latter species was then unknown there.

Numerous speltoids, many of which are chimeras, have been obtained after irradiation, aging, centrifuging and other treatments of *T. vulgare* seeds (17, 18, 37, 38, 39, 153, 159), and others. These mutants were for the most part chromosomal aberrants. Nilsson (123) obtained some indication that the physiological upset caused by bunt (*Tilletia*) may induce speltoid mutations, and Mr. E. S. McFadden, U.S.D.A., has evidence that frost during the flowering period may induce them (personal communication).

Part Mutations

The complete speltoid mutation involves the appearance of awns (which in wheat are a prolongation of the tip of the flowering glume or lemma) as well as modifications of the empty or outer glumes and of the rachis, which are described above. But beardless speltoids and bearded and half-bearded normals also arise from ordinary so-called "beardless" wheats. "Beardless" is here used in its popular sense to describe the common type of wheat which should strictly be classed as "tip-awned" (see 208). Truly beardless varieties of wheat are rare. Nilsson-Ehle called the bearded speltoids "total-mutations" and the others "part-mutations". At first he thought that the part-mutations were relatively infrequent and that their appearance was secondarily related to the total speltoid mutation. In a later study (131), however, he reported that the part-mutations are not at all infrequent and that in one strain they appear unaccompanied by bearded speltoids.

In bearded speltoids that arise directly and at one step by mutation there is complete linkage between awns and speltoid glumes: In crosses with beardless normals only beardless normal, beardless het speltoid and bearded speltoid progeny appear in F_2; the oc-

casional appearance of bearded het speltoids is due either to natural crossing or to a new mutation or aberration (see later), not to ordinary crossing-over. In back-crossed interspecific hybrids (*T. turgidum* × *T. vulgare*) × *T. turgidum,* Watkins (204) found about 39% crossing-over between awns and glume characters. In crosses between a beardless speltoid found in Panzerweizen and the parental stock, which is "bearded normal", Nilsson-Ehle's data (131) show about 23% crossing over (his analysis is in terms of gametic ratios). The bearded speltoids that arose through crossing over are vigorous plants. In the F_2 of a "half-bearded" normal × beardless speltoid, Nilsson-Ehle notes that the characters bearded, half-bearded and beardless behave as if they were allelomorphs in that whichever pair are crossed together only two types of progeny occur in F_2 and these in a 3 : 1 ratio. He points out, however, that the difference in linkage values, which appears to be significant, indicates that they cannot be due to simple multiple allelomorphic genes. He concludes that the bearded character in part-mutants is itself due to a complex of genes which are completely linked, as are the beard and glume genes (or gene complexes) of the total speltoid mutation; bearded, half-bearded and beardless simulate a multiple allelomorphic series of single genes because the mutation by affecting an interstitial segment prevents crossing over between the component factors of the bearding complex. It will be seen later how strikingly these concepts from purely genetic data can be fitted into the cytogenetic interpretation derived from later studies —hence this extensive consideration of Nilsson-Ehle's data and conclusions.

Compactoids, Subnormals and Associated Types

There remain for consideration here those mutants of *T. vulgare* which resemble *T. compactum.* These arise in the heterozygous form variously termed "compactum heterozygote", "subcompactum" or "subcompactoid". For the most part they occur as rare but regularly appearing offspring of Series β het speltoids. Lindhard (105, 106) found 184 in a total of 39,146 progeny from such het speltoids, and Nilsson-Ehle obtained 24 in a total progeny of 2,830. They also occurred twice in the progeny of Series γ het speltoids that had just changed over from Series β. They occur also, though very rarely, as mutants directly from *T. vulgare* and as sporadic

segregates from intervarietal or interspecific crosses involving *T. vulgare* (see 13, 45). They have never arisen from speltoids.

Subcompactoids regularly segregate still denser-headed types termed "compactoids". Distinction between subcompactoids and compactoids can at best be made only within individual strains, as the former may be denser in one strain than the latter in another. In general, the term "subcompactoid" is used for the regularly segregating types, and "compactoid" for their denser-headed segregates which can breed true, though owing to chromosome anomalies and natural crossing they often do not.

Subcompactoids may be grouped into three main segregation types. One, the simplest, gives only normal, subcompactoid and compactoid progeny. Another, the rarest type, gives in addition a small and irregular proportion of het speltoid offspring. A third, the commonest but most complex type, gives many het speltoids and also "square-head heterozygotes" or "sub normals" in addition to normals, subcompactoids and compactoids. The ratios are irregular and could not be understood until the chromosome constitution was determined (see Section D). Nilsson-Ehle (128, 129) devised various schemes involving partial heterogamy to explain the peculiar ratios, but later (131) stated that they had all been proved invalid. Lindhard (107) attempted an explanation on the basis of a pair of factors, L and l, which affect both the ear density and the progeny ratio. Since grossly abnormal chromosome behavior is now known to be involved, it is not surprising that these efforts, lacking cytological data, met with little success.

Lindhard's Series β het speltoids produced a number of other aberrant forms besides subcompactoids. These included: (*a*) a "perennis" type that produced a dense rosette of leaves, only rarely formed heads, and these very late and almost sterile; (*b*) a dwarf normal type; (*c*) a dwarf het speltoid; and (*d*) a very late-maturing type. The latter, "Spät Kolben", segregates its kind, and the perennis type in about equal numbers. The dwarf normal, "Zwerg Kolben", segregates its type and square-headed normals in either 1:1 or 1:4 ratios.

D. CYTOGENETIC STUDIES OF MUTANT WHEAT AND OATS

The genetic complexities outlined in the previous sections have largely been clarified by various cytogenetic studies dating from

1924 to the present. Cytogenetic analyses of *Triticum* and *Avena* which bear on the general problem may here be considered together, as they are in many respects parallel and in others complementary. Each genus has, of course, special cytogenetic features, and these are taken up in detail in the various papers cited and those of the writer and his associates now in press.

After many erroneous chromosome counts by earlier workers (nine had reported $2n = 16$ in *T. vulgare,* and as high as $2n = 48$ had been recorded in *Avena*), the correct numbers for *Triticum* were determined in 1918 (151, 154, 155) and for *Avena* in 1919 (96). Each genus contains three groups of species which are numerically diploids, tetraploids and hexaploids having $2n = 14$, 28 and 42 chromosomes.

It should be stressed that though *T. vulgare* and *A. sativa* are numerically hexaploid, their 42 chromosomes almost invariably form 21 bivalents and their genetic behaviour is correlatively like that of a true diploid in most respects. They are allopolyploids or amphidiploids which have doubtless arisen through chromosome doubling following interspecific hybridization (180). The ways in which such amphidiploids may differ from true diploids have been discussed by many authors including Stadler (166) and the writer (72) on cereals.

Winge (209) was one of the first to recognize the importance in plant evolution of chromosome doubling following hybridization. He was, in consequence, in a position to appreciate fully the cytogenetic possibilities inherent in *T. vulgare* when its polyploid nature was revealed and to speculate profitably, even though, in the light of subsequent discoveries, not always very accurately, on the significance of the aberrant chromosome numbers or behaviour that he found in various wheat mutants. Winge (210) reported that in speltoids obtained from Lindhard the normal chromosome number was present but that 19 bivalents and one quadrivalent ($19_{II} + 1_{IV}$), instead of 21_{II}, were occasionally formed at meiosis in pollen mother-cells. In het speltoids he occasionally found either a trivalent or an unpaired chromosome. In one of Lindhard's subcompactoids he could usually count only 41 chromosomes at anaphase, but at metaphase there sometimes appeared to be 21 bivalents. He eventually decided that there must be 42 chromosomes, of which one was usually a "vagabond" that got lost and degenerated in the cytoplasm leaving 20 to go at anaphase to one pole and 21 to the other. In

Lindhard's "squarehead heterozygote" (= "subnormal") he definitely found only 41 chromosomes. The "perennis type" also had only 41, these forming $20_{II} + 1_{I}$. A dwarf normal that segregated normals and dwarfs in a regular 3 : 1 ratio had the normal number of chromosomes which appeared at metaphase as 21_{II}.

Nilsson-Ehle and his associates had shown that many of the characters of wheat appear to be due to a balance between factors tending to push development in opposite directions. Winge, developing this concept further, argued that the "normal" phenotype of *T. vulgare* depends on a balance between factors on the three paired sets of chromosomes comprising its numerically hexaploid complement and that the various mutants, or "Aberranten" as he preferred to call them, are determined by changes in the balance of factors, brought about by aberrant chromosome conjugation and distribution.

If the seven pairs constituting a basic diploid set of *Triticum* chromosomes are represented as $\frac{1\,2\,3\,4\,5\,6\,7}{1\,2\,3\,4\,5\,6\,7}$, then the complement of *T. vulgare,* comprising three similar but not identical paired sets, may be represented as $\frac{1_A\,1_B\,1_C\,2_A\,2_B\,2_C}{1_A\,1_B\,1_C\,2_A\,2_B\,2_C} \cdots \frac{7_A\,7_B\,7_C}{7_A\,7_B\,7_C}$. Only one of of the triplicated pairs of chromosomes, say the $\frac{1_A\,1_B\,1_C}{1_A\,1_B\,1_C}$ group, appears to be significantly involved in the cytogenetics of speltoids and compactoids. We can therefore drop the numeral and refer to it as $\frac{A\,B\,C}{A\,B\,C}$. The C chromosomes of this group were postulated by Winge to carry factors pushing development towards the compactum type and the B chromosomes to carry factors tending towards speltoid or spelta. The normal phenotype of *T. vulgare* was assumed to be determined by the balance of factors on one pair of B and one pair of C chromosomes. Speltoids would then be produced by an excess of B chromosomes or a deficiency of C and compactoids by an excess of C or a deficiency of B. No definite function was assigned to the A chromosomes, and Winge did not distinguish *T. spelta* from speltoid.

Accepting $\frac{A\,B\,C}{A\,B\,C}$ as the relevant chromosome formula of *T. vulgare,* it is evident that chromosome A must normally pair only with

A, B with B and C with C, or true-breeding pure lines could not exist. But, Winge argued, B and C, though not identical, are sufficiently similar to pair occasionally. When bivalents AA, BC and BC $\left(\frac{A\,B\,B}{A\,C\,C}\right)$ or the quadrivalent BCBC $\left(\frac{A\,B\,B}{A\,C\,C}\right)$ are formed, gametes ABB and ACC obviously may result. If these are fertilized by normal ABC gametes the zygotes $\frac{A\,B\,B}{A\,B\,C}$ and $\frac{A\,C\,C}{A\,B\,C}$ will be produced. These would be the 42-chromosome het speltoid and the subcompactoid. The three B chromosomes of $\frac{A\,B\,B}{A\,B\,C}$ could then form the trivalent, and C be the unpaired "vagabond" he saw occasionally in het speltoids. He expected some het speltoids to have only 41 chromosomes, $\frac{A\,B\,o}{A\,B\,C}$, but did not find any of this type. The B chromosome of $\frac{A\,C\,C}{A\,B\,C}$ was assumed to be the "vagabond" in his subcompactoid. Because the "squarehead heterozygote" was almost normal *T. vulgare* in phenotype, though it had only 41 chromosomes, its constitution was assumed to be $\frac{A\quad B\quad o}{A\,(BC)\,C}$, in which the (BC) chromosome has originated by abnormal crossing-over between B and C.

On Winge's hypothesis subcompactoids should arise with the same frequency as het speltoids. They do not, and the only one of the formulae fully established today is $\frac{A\,B\,o}{A\,B\,C}$ which Winge expected but did not find. It is the constitution of a Series β het speltoid. Yet Winge's ideas have undoubtedly helped greatly in the elucidation of the general problem. Nilsson-Ehle (131) showed the difficulties that part-mutations create for Winge's theory, but he considered that it might explain many of the genetic complexities previously inexplicable. He recorded, however, that H. Ekstrand had examined his α, β and γ Series speltoids and found only normal chromosome numbers and behaviour in all of them.

Almost coincidently with Winge, Goulden (57) had begun cytogenetic studies of dwarf wheats and fatuoid oats, and shortly afterwards Huskins (65), at the suggestion of Dr. J. R. Fryer, had independently begun cytogenetic studies of fatuoids. Though only

Series α fatuoids had previously been known, 20 het fatuoid plants that developed from off-type seeds picked out by Goulden from supposedly pure-line Banner oats comprised three ratio-types. One produced more or less equal proportions of het fatuoids and dwarf fatuoids. The latter were the only plants he studied cytologically. They had extremely irregular pairing in pollen mother-cell meiosis, and this prevented an accurate chromosome count being made. Goulden attempted to apply Winge's concepts to the behaviour of certain dwarf wheats. Regarding the dwarf oats, he concluded that insufficient data were available for a sound explanation of their occurrence and behaviour, but suggested that "the cytological irregularities indicate that something is lacking which has a profound influence on the co-ordination of the chromosomes during reduction division. This may be either a single factor, a part of a chromosome containing several to many factors, or one or more whole chromosomes. The fact that all the dwarf plants are false wild seems to indicate that at least a part of a chromosome which also carries the cultivated factor has somehow been lost". We now know that "false wild" dwarfs of this type have only 40 chromosomes.

Huskins' (65, 66) first studies were on Series α fatuoids and het fatuoids obtained by crossing them with normal oats. Chromosome irregularities were found which suggested that "some chromosomal aberration, rather than a change in a single gene, is instrumental in causing the appearance of fatuoids". The extension of Winge's theory to fatuoids was favoured, though it was felt that "it is not clear how all the irregularities could be explained on this basis". In immediately succeeding studies, Huskins (67, 69–71) examined α, β and γ Series speltoids obtained from Nilsson-Ehle and Åkerman. He found also that a large collection of fatuoids, obtained from various sources, comprised three essentially similar Series. In 11 strains of Series α fatuoids and speltoids the normal chromosome number was found in all classes of segregates, but in het speltoids and het fatuoids a trivalent and a univalent was occasionally found. In speltoid and fatuoid segregates a quadrivalent sometimes occurred, as Winge had found in the Series α speltoids which he obtained from Lindhard. Series β het fatuoids and het speltoids were found by Huskins to have only 41 chromosomes, and these regularly formed $20_{II} + 1_{I}$ at pollen mother-cell metaphase. The chromosome constitution of γ Series strains proved very difficult to

determine. Counts varying from 41 to 43 were made in both het fatuoids and het speltoids. In some fatuoid and speltoid segregates of Series γ only the normal chromosome number could be found, but in a few cells of several different plants 44 were counted. It was decided that the higher counts must be the correct ones and that technical difficulties were preventing a full count in those that appeared to have fewer than 44. The conclusion was therefore reached that the constitutions of het speltoids and het fatuoids of the α, β and γ Series were, respectively, $\frac{A\,B\,B}{A\,B\,C}$, $\frac{A\,B\,o}{A\,B\,C}$ and $\frac{A\,B\,C\,B}{A\,B\,C}$, while the speltoid and fatuoid segregates from them were $\frac{A\,B\,B}{A\,B\,B}$, $\frac{A\,B\,o}{A\,B\,o}$ and $\frac{A\,B\,C\,B}{A\,B\,C\,B}$. A part-chromosome deficiency was observed in one Series γ het speltoid, but it was not thought related directly to the speltoid problem, as it was later found to be.

These early observations of the writer, like those of Winge and Goulden, were made on paraffin-embedded and sectioned material. In them the analysis of irregular configurations and behaviour is very difficult when the chromosome number is as high as in hexaploid wheat and oats. Since 1929 his studies and those of his associates have almost all been on permanent smear preparations. In these, Series γ het speltoids and fatuoids characterized by the deficiency of part of a chromosome, rather than by an extra one, were soon found (75, 76). The same observation was independently made shortly afterwards (134, 135, 192, 193). Though counts of 43 chromosomes have been made in Series γ het speltoids by the writer as well as others (18, 58, 120), it now appears certain that these were either erroneous interpretations, or that extra chromosomes other than those affecting the speltoid complex were present. The latter is definitely the case in some of the writer's plants which have been re-examined and further analyzed. Håkansson (58) at first interpreted certain configurations as heteromorphic bivalents of which one member had lost a large segment. He later decided that they were probably trivalents composed of three small chromosomes of equal size. His first impression now appears to have been correct. The error is readily explicable: the normal C chromosome has a sub-median "attachment" constriction dividing it into two "arms"; when most of one arm is missing, as the longer one is in

some γ strains, including that studied by Håkansson, the conjugation of a two-armed normal chromosome with a deficient one-armed C chromosome gives a three-partite body that may easily be mistaken for a trivalent composed of three small whole chromosomes. Müntzing (120), though he did not find the deficiency now known in the C chromosome of Series γ speltoids, stressed the probable significance of that illustrated by Huskins (71). The characteristic complement of Series γ het speltoids or het fatuoids is now known to be 20 normal bivalents and a heteromorphic bivalent composed of one normal C chromosome and one C visibly deficient at metaphase. The deficiency ranges in length from the whole of the longer arm to a segment on the limit of microscopic detectability. This segment must normally carry factors that prevent expression of the speltoid or fatuoid phenotype (76, 81, 82, 84, 111, 113, 134, 135, 152, 164, 192, 197). The chromosome number 41 found (198) in a het speltoid from Philiptschenko's (143) Series γ was evidently that of one of the Series β het speltoids which are regularly segregated by γ Series strains (82). The chromosome constitution now established for various oat and wheat mutants are shown diagrammatically in Figures 3 & 4.

Nishiyama (133) made extensive cytological studies of three Series α fatuoid strains obtained from the writer. While occasional unpaired chromosomes, trivalents and quadrivalents were found, Nishiyama concluded that the meiotic irregularities bore no relation to the plant phenotype and therefore gave no basis for the Winge-Huskins scheme of whole B and C chromosome substitutions. Uchikawa (197), from detailed cytogenetic studies of all three types of speltoids, reached the same conclusion. The total frequency of irregularities found by both Nishiyama and Uchikawa is, however, much lower in all classes of segregates than that observed in some pure varieties and many hybrids as well as in mutants of wheat and oats by many prior and subsequent workers (see 20, 95, 114, 179, 199). The Japanese workers have used paraffin-sectioned material, and it is the opinion of the writer that their observations are limited thereby, though they appear to be among the most accurate and detailed ever made in cereals by the older methods.

There is no doubt that some of the writer's (69–71) original figures of multivalent configurations in Series α were erroneous

interpretations of interlocked bivalents or of bivalents with unterminalized chiasmata. Most of them, however, on re-examination are considered probably correct, and the same may be assumed for the observations of Winge, Müntzing, Håkansson and others. The

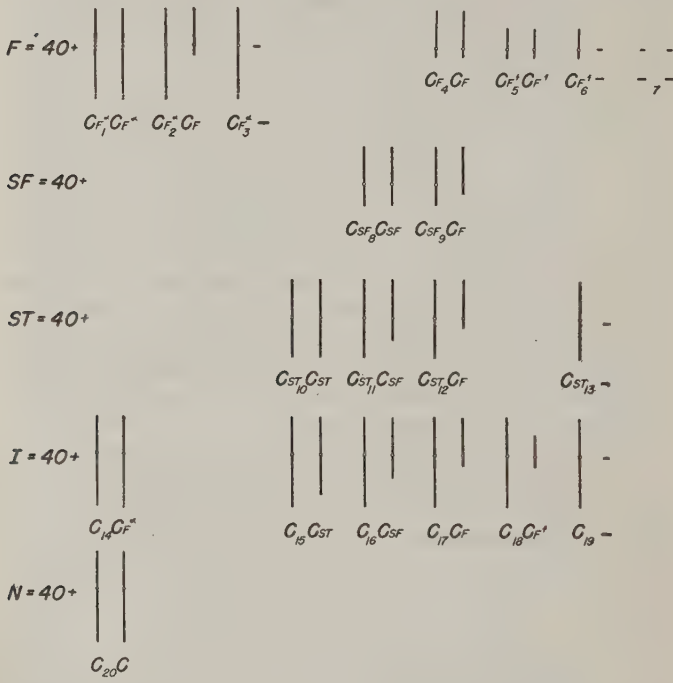


Fig. 3. Diagrammatic representation of the chromosome constitutions of fatuoids (F), subfatuoids (SF), steriloids (ST), intermediate or heterozygous mutants (I) and normal oats of *Avena sativa* L. or *A. byzantina* Koch. Normal oats in these hexaploid species have 42 chromosomes (21_{II}). The above forms are shown as having 40 chromosomes plus (or lacking) various modified forms and numbers of the "C" chromosome which carries factors that primarily determine the glume and awn characters.

question is, how significant are they for the fatuoid or speltoid problem? If Series α arises through "loss mutation", as do Series β and γ, but by a smaller minute deficiency that is not detectable microscopically by present methods, then multivalent formation in mutants of this Series is no direct indication of their constitution.

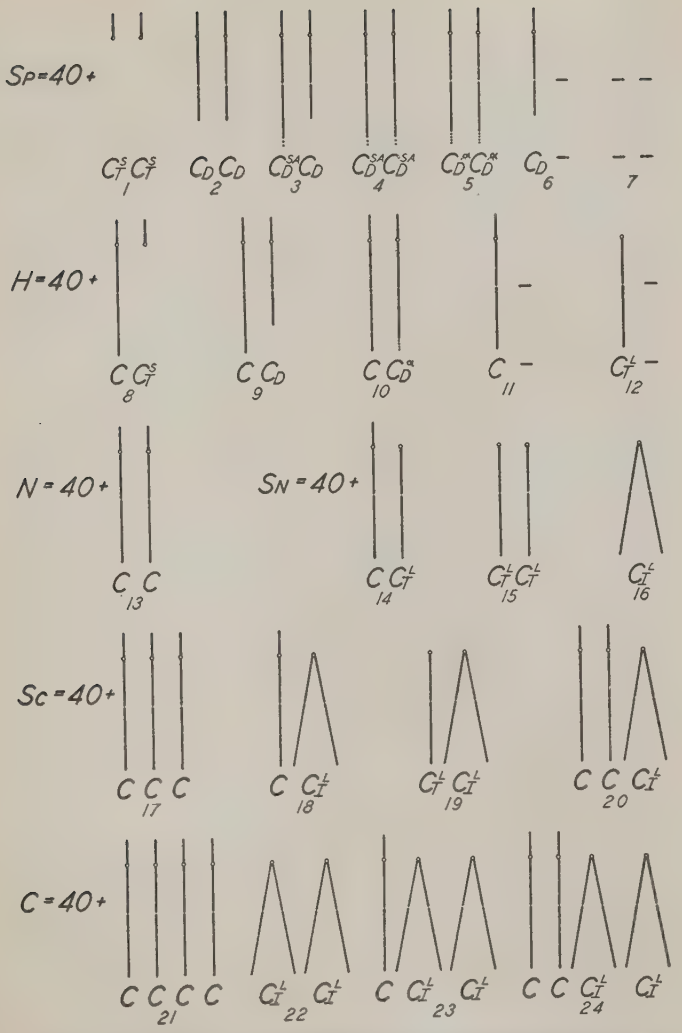


FIG. 4. Diagrammatic representation of the chromosome constitutions of speltoid (Sp), heterozygous speltoid (H), normal (N), subnormal (SN), subcompactoid (Sc) and compactoid (C) forms of common wheat. Normal wheats of any of the hexaploid species have 42 chromosomes (21_{II}). The forms above are shown as having 40 chromosomes plus (or lacking) various modified forms and numbers of the "C" chromosome which carries factors that primarily determine the normal glume, awn, and head-shape of common wheat.

It does, however, reveal the capacity for irregular pairing which exists in *T. vulgare* or *A. sativa,* and this remains one of the most likely mechanisms for the production of such chromosome mutations. The most abundant and definite evidence of multivalent formation found by Huskins (71) was in a "speltoid" strain that he suspected of being the derivative of a cross with *T. spelta,* as it has since been proved to be. It is rather ironical that the present re-analysis of Lindhard's and Winge's papers has led to the suspicion that the "speltoids" in which Winge found the multivalents, from which he formulated his theory of the origin of speltoids, were possibly also *T. spelta* hybrids (see 77). If they were not, the most plausible assumption is that extra chromosomes other than C were present in these lines. Such have been found in many of the writer's strains. In either case, frequent multivalent chromosome associations would be expected. It appears significant that Winge found no multivalents in a Series α strain that he obtained from Åkerman, and that Lindhard reported that his "speltoids" had hard and tight glumes like those of typical *T. spelta.* In a personal communication to the writer in 1927 he went further and expressed the opinion that there is no difference between speltoid and *T. spelta.* This conclusion is unacceptable (see 205), but it would come naturally to Lindhard if the vigorous segregates which he quite naturally considered to be speltoids, and from which he gave cytological material as such to Winge, were really *T. spelta* hybrids.

In any event it is apparent that these speltoids of Lindhard's on which Winge based his theory were not typical Series α mutants in either their genetic or cytological behavior, and the present general conclusion is that Series α speltoids and fatuoids are not specifically characterized by a multivalent chromosome association. But this does not mean that Winge's theory of origin through pairing of non-homologous (or, better, "homoeologous")[3] chromosomes, is necessarily invalid. Multivalents are indeed formed occasionally in all oats and wheat whether mutant or normal, and Watkins (206) and others have shown genetically that autosyndesis, which is the equivalent of the B + C pairing postulated by Winge, occurs regu-

[3] Homoeologous chromosomes (73) are those which are phylogenetically alike in a polyploid species. They once were homologous or identical but are now only similar, being sufficiently alike to synapse occasionally and so to form multivalent associations but not to pair regularly—homology though essential for regular pairing and crossing over does not, of course, in itself ensure pairing!

larly in certain tetraploid hybrids. In 0.3% of Uchikawa's (197) 41-chromosome Series β het speltoids a trivalent was formed and no univalents were present. In this material the C chromosome must have been paired with a non-homologous or homoeologous pair, though the significance of this appears to have been overlooked by Uchikawa. When Winge presented his hypothesis the chromosome was commonly considered a more unitary structure with respect to pairing than it is now known to be. We now stress synapsis between segments of chromosomes, but the associations formed by any segment affect the pairing possibilities of its neighbours. The "pairing block" (35), a dynamic entity, is now generally considered the functional unit.

Series γ fatuoids and speltoids are undoubtedly due to genetic deficiency, determined by the various segmental chromosome losses seen in different strains of Series γ, and there is every gradation between the loss of a whole C chromosome in Series β to the minute deficiencies found in some Series α strains. In most Series α strains, however, no deficiency can be observed in the chromosomes at metaphase, and the question then arises whether we are dealing with a gene mutation affecting the epistatic factors of the C chromosome or with the loss of them. For this we turn to genetic evidence.

The argument of Nishiyama (135), Uchikawa (197) and of Jones in his earlier work (89) that Series α must be due to gene mutation and not chromosome aberration (as are Series β and γ) can not be held as a necessary conclusion from their extensive genetic and cytological observations. The speltoid mutation involves at least two genes, or, more probably, two complexes of genes—those affecting glume and awn characters. In addition, there is between these two genes or gene complexes, an interstitial region, 30–40 crossover units long, which must be involved in the mutation. Were it not, part-mutants would regularly arise from het speltoids through crossing over in this region. The general concept of gene mutation certainly does not embrace such complex changes as those here involved, and Uchikawa's conclusion that Series α speltoids arise by gene mutation is therefore quite unacceptable. For fatuoids, however, the gene mutation theory can not as yet definitely be discarded. The fatuoid complex of characters is determined by either one gene or one complex of genes within which no crossing over has been established. The subfatuoid and steriloid mutations

are not yet proved to be changes necessarily involving different loci from the fatuoid mutation; they could, on present evidence, be multiple alleles, that is, different changes at a single locus. They have, however, at least been accompanied by different visible changes in the C chromosome in all the cases so far studied by the writer and his associates, and this together with all the other accumulated evidence makes chromosome mutation, such as deficiency, a far more plausible explanation of their origin than gene mutation.

If simple deficiencies are involved, as suggested (9, 76, 91, 120), these could owe their origin to the presence of a duplicated segment in the normal C chromosome. Huskins and Smith (83) have found that the single C chromosome in Series β het speltoids sometimes pairs on itself. This is evidence of segmental duplication within the C chromosome, and it provides a possible mechanism for the origin of deficiencies through irregularities in synapsis and crossing over. Pairing between the C chromosome and one of its homoeologues A or B would also produce deficiencies. The single factor ratios obtained from crossing the cultivated types with either the "wild" or the mutant forms show that only one of the three homoeologues (C) bears the epistatic "suppressors" that determine the cultivated phenotype. Crossing over during homoeologous association could therefore produce a C chromosome lacking this segment but otherwise relatively unchanged. Homoeologous pairing as the basis for the mechanism which directly produces the mutants would fit more of the data than simple segmental duplication, but convincing direct evidence for it would be harder to obtain. Both may well be involved. Efforts to settle these questions from studies of the chromosomes at the pachytene stage, when they are longer and more distinguishable, have met with only limited success. The chromosomes are too numerous and too long. In a few pachytene preparations they are relatively much shorter and clearer and from these some evidence has been obtained (81, 82).

The chromosome numbers 41 and 40 of Huskins (69, 71) for heterozygous and "homozygous" mutants of Series β have been confirmed for speltoids (58, 59, 117, 120, 147, 164, 165, 197) and for fatuoids (133). The genetic ratios of Nishiyama's 41-chromosome het fatuoids, like those of Goulden (57) and of the strains described elsewhere (80) and herein as "modified Series β" ("β

mod."), differ, however, from those of ordinary Series β het speltoids or fatuoids, though they are cytologically similar. They produce few normals, many 41-chromosome het fatuoids and many 40-chromosome dwarf sterile fatuoids.

From counts of chromosomes left out of pollen tetrad nuclei, it is possible in Series β to determine the proportion of gametes with 20 or 21 chromosomes (71). Nishiyama (133) calculated that in his 41-chromosome modified β het fatuoids it was 1:6. He assumes that: (*a*) female gametes are produced in the same ratio, (*b*) that all gametes function in the proportions they are formed, and (*c*) that the relatively low fertility of these het fatuoids is due to the death of many 40-chromosome fatuoid embryos. On these assumptions good agreement is reached between expectation and the actual genetic ratios. But the explanation seems an over-simplification (Sander, 152). It is, however, clear that in modified Series β the 20-chromosome gametes function readily, whereas in ordinary Series β het fatuoids, and Series β het speltoids also, the 20-chromosome pollen grains have a very low functioning capacity in competition with normal grains (164, 165, 197).

Nishiyama confirmed the observation of others (57, 69, 70, 79) that absence of both C chromosomes causes faulty meiotic pairing, and he attempted to locate on C the factors necessary for normal pairing. The analysis was based on fertile, tall fatuoids, having normal chromosome pairing, which are found occasionally in the progeny of modified β het fatuoids. These fatuoids have $20_{II} + 1_{I}$ instead of the usual 40_{I} of Series β or β mod. fatuoids. The univalent chromosome has a sub-median "attachment". It is smaller than the normal C chromosome and was proved by its behaviour in crosses with normals to be part of it. Nishiyama (135) believes that this univalent is the longer arm of a C chromosome and that the normal C therefore bears a factor or factors necessary for synapsis on its long arm and factors that suppress the fatuoid characters on its shorter arm. This interpretation involves, however, the formation of a new spindle attachment in a chromosome fragment and also other assumptions that do not appear to be valid (152). There is, however, complete agreement among the various workers that the essential cytological characteristic of both Series β and modified β is the loss of a C chromosome. The problems remaining are the location of various factors on it and the

cause of the difference between Series β and modified β in the functioning of their 20-chromosome male gametes.

Subcompactoid wheats from Nilsson-Ehle and Åkerman were studied cytologically by Håkansson (58, 60). He found two chromosome types. The less frequent type has an extra C chromosome, its formula being given as $20_{II} + 1_{III}$ or $\frac{A\,B\,C\,C}{A\,B\,C}$ (and that of its compactoid segregates as $\frac{A\,B\,C\,C}{A\,B\,C\,C}$). The commoner type has $20_{II} + C + Co$, or $\frac{A\,B\,C}{A\,B\,Co}$, (with its compactoids $\frac{A\,B\,Co}{A\,B\,Co}$), in which "Co" is a "compactoid producing" chromosome with duplicated ends. It was observed by S. G. Smith and the writer (76) and later others (95, 164, 194). As it is known now to be an "isochromosome" composed of a duplicated longer arm of the C chromosome, it is designated Cil.

When not paired with the normal C chromosome (called "No" by Håkansson) the duplicated arms of Cil pair and form chiasmata. and it therefore looks like a small bivalent. When C and Cil are paired they form a heteromorphic "bivalent," and at anaphase go to opposite poles forming gametes with 20 + C and 20 + Cil chromosomes. When unpaired, either C or Cil or both may be left out of the spore nuclei and gametes with only 20 chromosomes thus be formed. These fertilized by normal gametes produce the β het speltoids which are regular segregates from C Cil subcompactoids. Håkansson suggested that plants with 20_{II} + Cil must also occur and expected that these would be intermediate between compactoid and normal, *i.e.*, the "squarehead heterozygotes" of Lindhard, or "subnormals" as they are termed herein. This has been confirmed (83, 164, 165, 194–196). Huskins and Smith (83) have also found C C Cil subcompactoids which were expected but not found by Håkansson, and have confirmed his observation of Cil Cil compactoids. They have found, in addition, an unbalanced C Cil Cil compactoid. Håkansson noted that C Cil subcompactoids from Nilsson-Ehle had a shorter C chromosome than those from Åkerman. It appears to be the same as the "Ctl" chromosome of Huskins and Smith (83) which is the "telokinetic" or terminally attached long arm of C, which equals one-half of a Cil chromosome. The het speltoid progeny from subcompactoids of this type possess

20_{II} + Ctl, and consequently differ from ordinary Series β het speltoids in segregating subnormals (20_{II} + Ctl Ctl) instead of true normals (20_{II} + C C).

The steriloid and subfatuoid mutations may provisionally be considered part-mutations of the fatuoid complex. The same chromosome, C, is affected, and they behave like a multiple allelomorphic series with fatuoid, yet are evidently due to or at least associated with chromosome aberrations and may therefore involve different parts of a gene complex. Different sized deficiencies are involved in some cases and there are different ratio-types, as in fatuoids (80).

The relation of these various wheat and oat mutants to similar forms which segregate from interspecific hybrids has been investigated extensively (*e.g.*, 91, 104, 136, 146, 205, 206). From data on chromosome numbers and behavior, chromosome mutations and the genetics of interspecific crosses, many attempts have been made to reconstruct the phylogeny of the genera *Triticum* and *Avena* (see 46, 48, 56, 97, 115, 156, 181, 200, 205). The more detailed cytogenetic data now available on the various mutants may throw further light on these problems.

E. GENERAL CONCLUSIONS

Many off-types found in cultivated varieties of wheat and oats are definitely mutants, while others are the product of natural crosses. The types commonly described as false wild oats or fatuoids are mutants. The thesis that they arise through natural crossing between *A. sativa* and *A. fatua* is not maintained by any of the data marshalled in its support when these are critically examined. On the other hand, it is clear that some off-types which are almost indistinguishable from true mutant fatuoids, are natural hybrids or their descendants.

Speltoid wheats arise by mutation from *T. vulgare,* but, again, forms possessing either the same or a very similar complex of glume and spike characters arise as irregular segregates from various intervarietal and interspecific crosses between hexaploids or as regular segregates from the pentaploid hybrid *T. vulgare* × *T. turgidum*. The definitions of fatuoids and speltoids emphasize that they resemble the parent variety excepting in the one complex of characters and (occasionally) others genetically and developmentally associated with it. The type of mutation involved is definitely

chromosome mutation in most off-type wheats and oats studied. The diverse chromosome aberrations producing different ratio types are alike in that they all involve the loss of genes that ordinarily prevent the expression of the fatuoid or speltoid characters.

Pairing between "homoeologous" chromosomes of different sets or genomes in allopolyploid or amphidiploid species and the consequent establishment of new chromosome and genic balances was the basis of Winge's and Huskins' earlier theories of the origin of various wheat and oat mutants. This surely occurs, as evidenced genetically by the occurrence of "shift" and allied phenomena in polyploid wheat hybrids. But whereas the earlier development of the theory emphasized whole chromosome substitution as the result of homoeologous pairing, it now appears that much more emphasis should be laid on the secondary effect of irregular pairing in producing segmentally altered chromosomes and also on the fact that polyploidy permits the survival of chromosomally aberrant or segmentally deficient or duplicated types of gametes and zygotes that could not survive in dipolids.

Most of the striking mutations of wheat and oats appear to be caused by whole or part deficiencies or duplications of one particular chromosome, designated C. On this C chromosome there are factors affecting most of the characters which distinguish the different hexaploid species of each genus. The C chromosomes carry also colour and disease-resistance factors in some strains, and their absence affects the growth habit of the plant and in oats causes meiosis to be disrupted. They profoundly affect vigor and fertility. Albinism and a leaf-width mutation in oats (144, 146), a white chaff mutation in wheat (112) and hairy stem in wheat-rye hybrids (95) have all been shown to be associated with aberrations of particular chromosomes other than C. By contrast there are, in both oats and wheat, chromosomes which can be lost without causing any apparent effect beyond a slight reduction in size and fertility. Sears (160–162) found that most but not all chromosomally aberrant wheats obtained from a "haploid" *T. vulgare* were morphologically distinguishable from the normal,[4] and O'Mara (140)

[4] In an elegant analysis which has appeared since this manuscript was prepared (Genetics 29: 232–246. 1944), Sears has shown the contributions made by 17 of the 21 pairs of chromosomes to the phenotype of *T. vulgare* var. Chinese Spring. When both members of the pair are absent all 17 chromosomes analyzed cause appreciable deviation from the normal, but, provided the plants are grown under favorable conditions, only two chromo-

found that of three extra rye chromosomes present in an amphidiploid wheat-rye hybrid backcrossed to wheat, two produced definite effects and the third apparently none. Irregularities in the number and behaviour of relatively non-effective or "extraneous" chromosomes are common in many mutants of the speltoid and fatuoid series. They are responsible for some of the difficulty experienced by various workers attempting to analyze these problems.

Apart from the immediate problems of the origin of speltoid, fatuoid and related mutants and their diverse genetic behavior, which are reviewed herein, the cytogenetic analysis of these forms has given data which bear on problems of chromosome mechanics, especially in polyploids, on pseudo-allelism and the concentration of genes on a single chromosome, on the significance of polyploidy in relation to mutation, the pure-line theory and plant-breeding practices, and on the evolutionary history of *Triticum* and *Avena*. These problems, merely outlined above, are considered in some detail elsewhere (81, 83).

F. SUMMARY

Fatuoids, speltoids and related oat and wheat mutants arise through chromosome aberration, and their diverse genetic ratiotypes are determined by their particular chromosome constitutions. These are shown diagrammatically in Figures 3 and 4.

(*a*) Loss of one C chromosome produces a Series β het fatuoid or speltoid. The remaining C chromosome, being univalent at meiosis, "splits" after the members of the bivalents have separated to the poles, but its halves often fail to be included in the daughter nuclei. The gametes therefore possess either 20 or 20 + C chromosomes, with a marked preponderance of the former. Female gametes of either constitution function readily, but male gametes lacking C rarely effect fertilization. The characteristic ratio of Series β, which is one normal to more than four heterozygotes (the number differs somewhat in different strains) is thus determined. Rarely, Series β het speltoids have 20_{II} and a C chromosome lacking the shorter arm ("Ctl" since it is the telomitic longer arm of C); they segregate subnormals (20_{II} + Ctl Ctl) instead of true normals.

somes show appreciable effects when only one member of the pair is lacking. One of these two is the C chromosome, which he designates number IX. He confirms the earlier observations, reviewed herein, that it carries factors for squareheadedness, narrow glumes and suppression of awns, and shows further that chromosome X also carries an awn suppressor, while factors for the promotion of awn development occur on chromosomes II and XX.

(*b*) Modified Series β strains have chromosome number and behavior the same as in typical Series β. Both female and male gametes lacking a C chromosome are, however, functional in these strains; many sterile, dwarf, 40-chromosome fatuoid progeny are therefore produced by modified β het fatuoids.

(*c*) Loss of an appreciable part of one of the C chromosomes produces Series γ het speltoids or het fatuoids; their formula is $20_{II} + C\ Cd$ (Cd = a chromosome having an appreciable deficiency). The size of the deficiency varies in different strains, and there may be a correlation between it and the genetic ratio. In most strains the C and Cd chromosomes pair and disjoin fairly regularly, and gametes with 20 + C and 20 + Cd are therefore formed in approximately equal numbers. Ovules of both types function readily, but pollen grains with 20 + Cd effect fertilization only rarely—hence the production of normal and het fatuoid progeny in ratios approximating 1 : 1. The few 20 + Cd male gametes which function and fertilize similar female gametes produce the few Cd Cd speltoid or fatuoid progeny. These are more or less dwarf and sterile. When the C and Cd fail to pair and behave as univalents, their halves frequently fail to enter the daughter nuclei. Gametes are therefore formed with only 20 chromosomes, and these fertilized by normal, 20 + C, gametes form the $20_{II} + C$, Series β, heterozygotes that occur with appreciable frequency in the offspring of Series γ het fatuoids or speltoids. A 20-chromosome gamete (lacking C) fertilized by a 20 + Cd gamete gives a 41-chromosome speltoid or fatuoid. In one γ speltoid strain the deficiency involves the whole of the longer arm of the C chromosome; the formula for the het speltoid is then $20_{II} + C + Cts$ (Cts = telomitic short arm of C).

(*d*) Series α het fatuoids or speltoids segregate as if they differed from the normal by a single unit factor, and it has therefore been argued that they arise by gene mutation. Few strains of fatuoids and almost none of speltoids, however, give good 1 : 2 : 1 ratios. There is nearly always a deficiency of the homozygous mutant progeny, and sometimes the ratio may be nearer 1 : 1 : 0 than 1 : 2 : 1. It is then a matter of definition whether they be classed as Series α or γ. Those giving ratios closely approaching 1 : 2 : 1 have no chromosome deficiency large enough to be detectable at meiotic metaphase. Some het speltoids which are intermediate and have by Nilsson-Ehle and others been classed as Series α have a visible

deficiency. The minimum deficiency involved is probably greater in the speltoid total-mutation, since it involves two genetically separable genes or gene complexes, than in the fatuoid, which is apparently determined by one gene complex. The deficiencies observed could have arisen either through intrachromosome pairing of a duplicated segment which has been found in the C chromosome or through pairing between C and some other phylogenetically related chromosome. If caused by such "homoeologous" pairing, the deficiency may arise *de novo* or may be a transference to the C chromosome of a phylogenetically old relative-deficiency. The occurrence of "speltoids" as regular segregates from interspecific wheat hybrids bears on the latter point and also constitutes evidence, of an *a priori* nature, that whole chromosome substitution as first envisaged by Winge may possibly be one cause of true speltoid mutations, though the existence of such substitution speltoids is not yet definitely established. There is, however, no unequivocal evidence for one specific "B" chromosome carrying a complex of factors hypostatic to those of C and thus none for the original formulae of the Winge-Huskins hypothesis. The general basis of this hypothesis appears sound, but its detailed development has been greatly modified. The "speltoids" of hybrid origin and, even more, the *A. sativa* × *A. fatua* segregates often mistaken for fatuoids, must be considered as posing distinct problems to be related in a phylogenetic analysis, but not to be confused with mutants in any investigation of either.

(*e*) Steriloid and subfatuoid mutations involve deficiencies of different sizes in the C chromosome of *A. sativa*. Normal, steriloid, subfatuoid and fatuoid behave, however, as if they were due to descending members of a series of multiple alleles. The C chromosome carrying the "steriloid deficiency" occurs as a univalent in a modified β strain of steriloids. Segregating steriloids of this type are phenotypically identical with true-breeding steriloids. They have 41 chromosomes and give rise to a few 42-chromosome true-breeding steriloids, many segregating-steriloids and 40-chromosome dwarf fatuoids which lack the normal synaptic association of meiosis.

(*f*) Subcompactoids of the commonest type (Type 1) have a "Cil" chromosome; it is an "isochromosome" composed of a duplicated longer arm of the C. Their total complement is 20_{II} + C + Cil. Rarely, similar forms are segregated with 20_{II} + Ctl + Cil.

(*g*) "Subnormal" mutants have a Cil chromosome but lack a normal C. More rarely they have two separate Ctl chromosomes in place of a Cil chromosome (which is two united longer arms).

(*h*) A second type of subcompactoid is a "primary trisomic" having three C chromosomes—20_{II} + C C C.

(*i*) A third type of subcompactoid has 20_{II} + C C + Cil.

(*j*) Common types of compactoids have 20_{II} + Cil Cil, 20_{II} + C C C C, or 20_{II} + C + Cil Cil.

ACKNOWLEDGMENTS

I am indebted to Dr. H. G. Sander for much assistance in the reviewing of literature and the critical revision of this paper.

BIBLIOGRAPHY

1. Aamodt, O. S. *et al.* 1934. Natural and artificial hybridization of *Avena sativa* with *A. fatua* and its relation to the origin of fatuoids. Canad. Jour. Res. **11**: 701–727.
2. Åkerberg, E. 1936. Om fluorescensan hos gul-och vithavre samt hos vissa fatuoider. Nordisk Jordbrugsforskning. Kobenhavn 1936. No. 5–6: 313–321.
3. Åkerman, A. 1920. Speltlike bud-sports in common wheat. Hereditas **1**: 116–127.
4. ————. 1921. Undersökningar rörande flyghavrelika mutationer i vanlig odlad havre. Sver. Utsädesf. Tidsk. **31**: 266–268.
5. ————. 1923. Beiträge zur Kenntnis der Speltoidmutationen des Weizens. I. Untersuchungen über eine Speltoidform aus schwedischen Sammetweizen. Hereditas **4**: 111–124.
6. ————. 1927. Weitere Studien über Speltoidchimären bei *Triticum vulgare*. Hereditas **9**: 321–334.
7. ———— and Bader, M. 1937. Über Kreuzungen zwischen *Avena sativa* und *Avena fatua* und einige Untersuchungen über Fatuoiden. Zeit. Züchtg. A. Pflanzenz. **22**: 1–208.
8. Alabouvette, L. and Friedberg, R. 1936. Étude de quelques Avoines fatuoides. Ann. Ephiphyties et de Phytogénétique **1**(1934–1935): 1–21.
9. Armstrong, J. H. 1933. Cyto-genetic studies in *Matthiola* and *Triticum*. Ph.D. Thesis, McGill Univ.
10. Ascherson, P. and Graebner, P. 1898. Synopsis der mitteleuropäischen Flora. Vol. 2: 242–243.
11. Atwood, W. M. 1914. A physiological study of the germination of *Avena fatua*. Bot. Gaz. **57**: 386–414.
12. Becker, J. 1927. Handbuch des Getreidebaues. (Handbuch des gesamten Pflanzenbaues. Vol. 1).
13. Boshnakian, S. 1922. The genetics of squareheadedness and of density in wheat, and the relation of these to other characters. N. Y. (Cornell) Agr. Exp. Sta., Mem. **53**: 801–882.
14. Bridges, C. B. 1917. Deficiency. Genetics **2**: 445–465.
15. Buchinger, A. 1934. Vegetative Spaltung an dem Haferartbastard *Avena sativa L.* × *A. Strigosa* Schreb. Genetica **15**: 393–424.
16. Buckman, J. 1857. Report on the experimental plots in the Botanical Garden of the Royal Agricultural College at Cirencester. Rep. 27th Meeting, Brit. Assoc. Advt. Sci., Dublin: 200–215.

17. Bynov, F. A. 1938a. Les mutations de *Triticum vulgare* provoquées par un courant électrique. Trav. Jard. Bot. Univ. Moscow **2**: 17–35.
18. ————. 1938b. La centrifugation comme facteur de mutations. Trav. Jard. Bot. Univ. Moscow **2**: 36–46.
19. Callaghan, A. R. 1929. False wild oats. Agr. Gaz. New So. Wales **40**: 625–631.
20. Camara, A. de S. 1936. Notas sobre espeltoides. Rev. Agron. (Lisboa) **24**: 301–318.
21. Coffman, F. A. *et al.* 1925. A study of variability in the Burt oat. Jour. Agr. Res. **30**: 1–64.
22. ———— and Stanton, T. R. 1940. Dormancy in fatuoid and normal oat kernels. Jour. Am. Soc. Agron. **32**: 459–466.
23. ———— and Taylor, J. W. 1932. Prevalence and origin of fatuoids in Fulghum oats. Proc. 6th Int. Cong. Gen. **2**: 28–29.
24. ———— and ————. 1936. Widespread occurrence and origin of fatuoids in Fulghum oats. Jour. Agr. Res. **52**: 123–131.
25. ———— and Wiebe, G. A. 1930. Unusual crossing in oats at Aberdeen, Idaho. Jour. Am. Soc. Agron. **22**: 245–250.
26. Cooper, A. 1909. More about White "Wild" Oats. Nor'West Farmer, Winnipeg **28**: 1225.
27. Cosson, M. E. 1854. Classification des espèces du genre *Avena* du groupe de l'*Avena sativa* (*Avena*, sect. Avenatypus), et considérations sur la composition et la structure de l'épillet dans la famille des Graminées. Bull. Soc. Bot. France **1**: 11–17.
28 Crépin, C. 1921. Sur un hybride naturel entre *Avena fatua* et *Avena sativa* à glumelles jaunes. Ann. École Nat. Agr. Grignon **7**: 143–154.
29. ————. 1925. Hybridation naturelle chez l'avoine. Comp. Rend. Acad. Agr. France **11**: 974–978.
30. ————. 1927. Les fausses folles avoines; mutation ou hybrides? Zeit. Ind. Abs. Ver., Suppl. **1**(1928): 568–575.
31. Criddle, N. 1909a. The so-called white wild oats and what they are. Ottawa Nat. **23**: 127–128.
32. ————. 1909b. Some facts about wild oats. Nor'West Farmer, Winnipeg **28**: 1117–1118.
33. ————. 1910. The status of false wild oats. Canad. Seed Growers Assoc., Ann. Rep. **6**: 104–105.
34. ————. 1912. Wild oats and false wild oats. Dept. Agr. Canada., Bull. Suppl. **7**: 1–11.
35. Darlington, C. D. 1937. Recent advances in cytology. 2nd ed.
36. Darwin, Ch. 1868. Animals and plants under domestication.
37. Delaunay, L. N. 1930. Die Chromosomenaberranten in der Nackthommenschaft von röntgenisierten Ähren einer reinen Linie von *Triticum vulgare albidum* All. Zeit. Ind. Abs. Ver. **55**: 352–355.
38. ————. 1931. Resultat eines dreijährigen Röntgenversuches mit Weizen. Züchter **3**: 129–137.
39. ————. 1932. The X-ray mutations in wheat. Bull. (Trudy) Lab. Genetics (Akademiia nauk, Leningrad) **9**: 173–180.
40. Denaiffe, C. *et al.* 1927. L'Avoine. 2nd ed.
41. Derick, R. A. 1933. Natural crossing with wild oats, *Avena fatua*. Sci. Agr. **13**: 458–459.
42. ———— and Love, R. M. 1937. Artifically induced fatuoids in a dwarf mutant oat. Sci. Agr. **17**: 703–706.
43. Dow, G. 1910. The status of the false wild oat. Canad. Seed Growers' Assoc., Ann. Rep. **6**: 105–107.
44. Ducellier, L. O. 1923. L'hybridation du blé en Algérie. Formes speltoides and durelloides. Bull. Soc. Hist. Nat. du Nord **14**: 164–172.
45. Dumon, A. G. 1931. Speltoiden en compactoiden bij rassen van *Triticum vulgare*. Natuurwetenschappelijk T. **13**: 101–104.

46. Emme, E. K. 1934. Certain laws governing the inheritance of morphological characters in interspecific oat hybrids. Bull. Appl. Bot., Leningrad, 1934 **13**: 5–14.
47. Emme, H. 1931. Genetik des Hafers. Züchter **3**: 109–124.
48. ————. 1938. Evolution of oats of the section Euavena Griseb. Biologischeskij Zhurnal **7**: 91–122.
49. Fedorova, N. 1930. Hybridization of *Avena sativa* with *Avena fatua*. 1. Qualitative characters. Bull. Bur. Genet. (Leningrad) 1930 **8**: 47–61.
50. Fischer, M. 1900. Winterhafer. Fühling's Landw. Zeit. **49**: 718–723; 766–777; 806–810.
51. ————. 1902. Einige Nachträge über Pflanzenzüchtung. Fühling's Landw. Zeit. **51**: 411–415.
52. Florell, V. H. 1931. Inheritance of type of floret separation and other characters in inheritance crosses in oats. Jour. Agr. Res. **43**: 365–386.
53. Gante, T. 1921. Über eine Besonderkeit der Begrannung bei Fatuoid-Heterozygoten. Hereditas **2**: 410–415.
54. Garber, R. J. 1922. Origin of false wild oats. Jour. Hered. **13**: 40–48.
55. ———— and Quisenberry, K. S. 1923. Delayed germination and the origin of false wild oats. Jour. Hered. **14**: 267–273.
56. Gates, R. R. 1931. The origin of bread wheats. Nature **127**(3200): 325–326.
57. Goulden, C. H. 1926. A genetic and cytological study of dwarfing in wheat and oats. Minn. Agr. Exp. Sta., Tech. Bull. 33.
58. Håkansson, A. 1930. Zytologische Beobachtungen an s.g. Speltoid-heterozygoten beim Weizen. Svensk Bot. Tidsk. **24**: 44–57.
59. ————. 1931. Die Chromosomenzahl von Speltoidheterozygoten, die aus s. g. subcompactum-Typen beim Weizen hervorgegangen sind. Bot. Not. **1931**: 343–345.
60. ————. 1933. Zytologische Studien an compactoiden Typen von *Triticum vulgare*. Hereditas **17**: 155–196.
61. Harlan, H. V. 1929. The weedishness of wild oats. A reluctant and backbreaking study in adaptation. Jour. Hered. **20**: 515–518.
62. Haussknecht, C. 1885. Über die Abstammung des Saathabers. Mitt. Geogr. Ges., Jena **3**: 231–242.
63. Heribert-Nilsson, N. 1916. Eine mendelsche Erklärung der Verlust-mutanten. Ber. Deut. Bot. Ges. **34**: 870–880.
64. Howes, E. A. 1911. Wild oats. Thesis (unpubl.), Ont. Agr. Coll., Guelph, Ont.
65. Huskins, C. L. 1925. Chromosomes in *Avena*. Nature **115**(2897): 677–678.
66. ————. 1926. Genetical and cytological studies of the origin of false wild oats. Sci. Agr. **6**: 303–313.
67. ————. 1927a. The origin of fatuoids in cultivated oats. Nature **119**(2984): 49.
68. ————. 1927b. The elimination of false wild oats; a breeding possibility. Sci. Agr. **7**: 285–286.
69. ————. 1927c. On the genetics and cytology of fatuoid or false wild oats. Jour. Genet. **18**(3): 315–363.
70. ————. 1927d. Genetical and cytological studies of fatuoid oats and speltoid wheats. Proc. V. Int. Gen. Congr. (Zeit. Ind. Abs. Ver., Suppl. 1: 907–916).
71. ————. 1928. On the cytology of speltoid wheats in relation to their origin and genetic behavior. Jour. Genet. **20**(1): 103–122.
72. ————. 1929. Some aspects of polyploidy in relation to the cereal crops. John Innes Hort. Inst., Conf. Polyploidy 27–37; Sci. Agr. **10**: 313–320.

73. ————. 1931a. A cytological study of Vilmorin's unfixable dwarf wheat. Jour. Genet. **25**: 113–124.
74. ————. 1931b. Fatuoid oats. Baillière's Encyclopaedia of Scientific Agriculture. Vol. 2: 864–867.
75. ————. 1932. Factors affecting chromosome structure and pairing. Trans. Roy. Soc. Canad., III **26**, Sect. V: 17–28.
76. ————. 1933. The origin and significance of fatuoids, speltoids, and other aberrant forms of oats and wheat. Proc. World's Grain Exh. & Conf. Vol. 2: 1–6.
77. ————. Chromosome mutations in polyploid *Avena* and *Triticum* I. [In press].
78. ———— AND FRYER, J. R. 1925. The origin of false wild oats. Sci. Agr. **6**: 1–13.
79. ———— AND HEARNE, E. M. 1933. Meiosis in asynaptic dwarf oats and wheat. Jour. Roy. Micr. Soc. **53**: 109–117.
80. ———— *et al.* Chromosome mutations in polyploid *Avena* and *Triticum.* V. The cytogenetics of steriloid and subfatuoid Kanota oats. Canad. Jour. Res. [In press].
81. ———— AND SANDER, G. Chromosome mutations in polyploid *Avena* and *Triticum.* IV. The cytogenetics of fatuoid Kanota oats. Canad. Jour. Res. [In press].
82. ———— AND SMITH, S. G. Chromosome mutations in polyploid *Avena* and *Triticum.* II. The cytogenetics of speltoid wheats. Canad. Jour. Res. [In press].
83. ———— AND ————. Chromosome mutations in polyploid *Avena* and *Triticum.* III. The cytogenetics of compactoid wheats. Canad. Jour. Res. [In press].
84. ———— AND SPIER, J. D. 1934. The segregation of heteromorphic homologous chromosomes in pollen mother-cells of *Triticum vulgare.* Cytologia **5**: 269–277.
85. ISHIKAWA, K. 1934. Occurrence of speltoid mutants in some Japanese varieties of wheat. I–II. Agr. & Hort. Japan **9**: 1361–1371, 1556–1571, 2244–2247; Pl. Breed. Abs. **6**: 260.
86. IVANOV, F. 1930. On crosses of tetraploid oat forms (*Av. barbata Poll., Av. Brauni* Korn.) among themselves and with hexaploid forms (*Av. sativa* L., *Av. nuda* L. var. *inermis* Korn., *Av. Ludowiciana* Dur., *Av. sterilis* L.). Proc. U.S.S.R. Cong. Gen. Plant and Animal Breed. 1930. Vol. 2: 243–263.
87. JOHNSON, L. P. V. 1935. The inheritance of delayed germination in hybrids of *Avena fatua* and *A. sativa.* Canad. Jour. Res. **13**: 367–387.
88. JONES, E. T. 1927. Preliminary studies on the absence of yellow colour in fatuoid or false wild oats. Welsh Jour. Agr. 3: 221–231.
89. ————. 1930a. Morphological and genetical studies of fatuoid and other aberrant grain types in *Avena.* Jour. Genet. **23**: 1–68.
90. ————. 1930b. Yellow fatuoids in oats. Jour. Hered. **21**: 81–82.
91. ————. 1940. A comparison of the segregation of wild versus normal or cultivated base in the grain of diploid, tetraploid and hexaploid species of oats. Genetica **22**: 419–434.
92. KAJANUS, B. 1923a. Ueber Ährchenabstand und Ährchenzahl bei Nachkommenschaften von Speltoid-Heterozygoten. Hereditas **4**: 10–16.
93. ————. 1923b. Genetische Untersuchungen an Weizen. Bib. Genet. **5**: 1–187.
94. ————. 1927. Die Ergebnisse der genetischen Weizenforschung. Bib. Genet. **3**: 141–244.
95. KATTERMAN, G. 1937. Das Verhalten der Chromosomen für Behaarung roggenbehaarter Nachkommen aus Weizen Roggenbastardierung in neuen Kreuzungen mit Roggen und Weizen. Zeit. Ind. Abs. Ver. **74**: 1–16.

96. KIHARA, H. 1919. Über cytologische Studien bei einigen Getreidearten. II. Chromosomenzahlen und Verwandschaftsverhältnisse unter *Avena-Arten*. Bot. Mag. **33**: 95–98.
97. ———— AND MATSUMURA, S. 1940. Weitere Untersuchungen über die pentaploiden *Triticum*-Bastarde. XII. Schlussmitteilung. Jap. Jour. Bot. **11**: 27–39.
98. KOERNICKE, F. AND WERNER, H. 1885. Handbuch des Getreidebaues.
99. LATHOUWERS, V. 1921. Variations speltoides dans les lignées pures de froment et dans une "population" d'Epeautre. Bull. Soc. Roy. Bot. Belg. **54**: 218–228.
100. ————. 1924. Variations speltoides apparues dans les lignees pures de froment et d'épeautre. Comp. Rend. Assoc. Franc. Avanc. Sci. **48**: 1009–1113.
101. ————. 1925. Étude génétique de deux variations speltoides. Bull. Soc. Roy. Bot. Belg. **57**: 78–104.
102. ————. 1927. Étude de certaines variations speltoides apparues dans les lignees púres de froment. Verh. V. Int. Kongr. Vererb., Zeit. Ind. Abs. Ver., Vol. 2: 953–954.
103. ————. 1930. La variabilité (non fluctuante) dans un lignée de *Triticum vulgare*. Apparition de variantes "speltoides" steriles. Bull. Soc. Bot. Belg. **63**: 49–54.
104. LEIGHTY, C. E. AND BOSHNAKIAN, S. 1921. Genetic behaviour of the spelt form in crosses between *Triticum Spelta* and *Triticum sativum*. Jour. Agr. Res. **22**: 335–364.
105. LINDHARD, E. 1922. Zur Genetik des Weizens. Eine Untersuchung über die Nachkommenschaft eines im Kolbenweizen aufgetretenen Speltoidmutanten. Hereditas **3**: 1–90.
106. ————. 1923. Fortgesetze Untersuchungen über Speltoidmutationen. Begrannungs-Komplikationen bei Compactum Heterozygoten. Hereditas **4**: 206–220.
107. ————. 1927. Ueber Ährendichte und Spaltungsmodi der Speltoid-heterozygoten. Kung. Vet. Landb. Aarsskr. (Denmark) **1927**: 1–37.
108. LOVE, H. H. AND CRAIG, W. T. 1918. The relation between color and other characters in certain *Avena crosses*. Am. Nat. **52**: 369–383.
109. ———— AND ————. 1929. A note on yellow fatuoids. Jour. Hered. **20**: 172.
110. ———— AND FRASER, A. C. 1917. The inheritance of the weak awn in certain *Avena* crosses. Am. Nat. **51**: 481–493.
111. LOVE, R. M. 1935. Cytogenetic studies of steriloid and sub-fatuoid oats. Ph.D. Thesis, McGill Univ.
112. ————. 1938. A cytogenetic study of white chaff off-types occurring spontaneously in Dawson's Golden Chaff winter wheats. Genetics **23**: 157.
113. ————. 1940a. A cytologically deficient speltoid of hybrid origin. Genetics **25**: 126.
114. ————. 1940b. Chromosome number and behaviour in a plant breeder's sample of pentaploid wheat hybrid derivatives. Canad. Jour. Res. **18**: 415–434.
115. MALZEW, A. I. 1930. Wild and cultivated oats. Bull. Appl. Bot., Genet. & Plant Breed. Suppl. 38.
116. MARQUAND, C. V. B. 1922. Varieties of oats in cultivation. Univ. Coll. Wales, Welsh Pl. Breed. Stat., Aberystwyth, Bull. C **2**: 2–44.
117. MATSUMURA, S. 1939. The missing chromosome in B type speltoid wheats. Jap. Jour. Genet. **15**: 323–324.
118. MATSUURA, H. 1931. Genic analysis in *Avena*. Jour. Fac. Sci., Hokkaido Imp. Univ. V **1**: 77–107.
119. ————. 1933. A bibliographical monograph on plant genetics (1900–1929). 2nd ed. Hokkaido Imp. Univ.

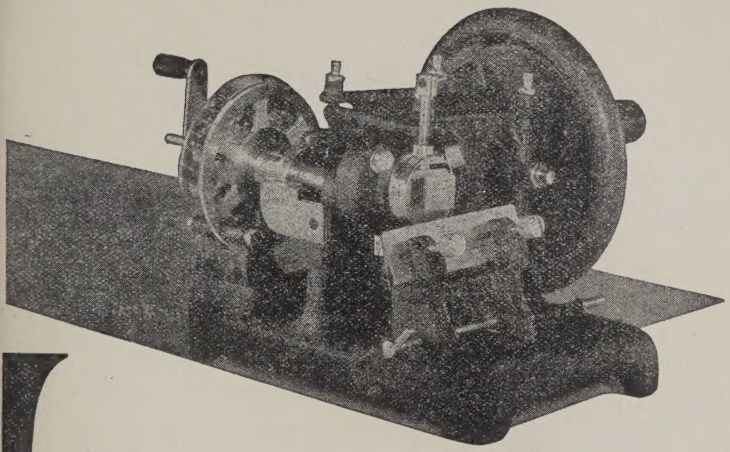
120. Müntzing, A. 1930. Einige Beobachtungen über die Zytologie der Speltoidmutanten. Bot. Not. **1930**: 35–47.
121. Newman, L. H. 1912. Plant breeding in Scandinavia.
122. ————. 1923. Origin of false wild oats. Sci. Agr. **3**: 169–170.
123. Nilsson, E. 1933. Paralleles Auftreten von *Tilletia*-Infektion und Speltoid-charakter bei *Triticum vulgare*. Hereditas **18**: 262–268.
124. Nilsson-Ehle, H. 1907. Om hafresorters konstans. Sver. Utsöderförenings Tidskr. **1907**: 227–239.
125. ————. 1911. Über Fälle spontanen Wegfallens eines Hemmungsfaktors beim Hafer. Zeit. Ind. Abs. Ver. **5**: 1–37.
126. ————. 1914. Über einen als Hemmungsfaktor der Begrannung auftretenden Farbenfaktor beim Hafer. Zeit. Ind. Abs. Ver. **12**: 36–55.
127. ————. 1917. Untersuchungen über Speltoidmutationen beim Weizen. Bot. Not. **1917**: 305–329.
128. ————. 1920. Multiple Allelomorphe und Komplexmutationen beim Weizen. (Untersuchungen über Speltoidmutationen beim Weizen. II.) Hereditas **1**: 277–311.
129. ————. 1921a. Über mutmässliche partielle Heterogamie bei den Speltoidmutationen des Weizen. (Untersuchungen über Speltoidmutationen beim Weizen. III.) Hereditas **2**: 25–76.
130. ————. 1921b. Fortgesetzte Untersuchungen über Fatuoidmutationen beim Hafer. Hereditas **2**: 401–409.
131. ————. 1927. Das Verhalten partieller Speltoidmutationen bei Kreuzung untereinander. (Untersuchungen über Speltoidmutationen beim Weizen. IV.) Hereditas **9**: 360–379.
132. Nilsson-Leissner, G. 1925. Berträge zur Genetic von *Triticum spelta* and *T. vulgare*. I. Hereditas **7**: 1–74.
133. Nishiyama, I. 1931. The genetics and cytology of certain cereals. II. Jap. Jour. Genet. **7**: 49–102.
134. ————. 1933a. The genetics and cytology of cereals. IV. Jap. Jour. Genet. **8**: 107–123.
135. ————. 1933b. On the mechanism of the fatuoid and speltoid mutation. Kwagaku (Japan) **3**: 147–152; Pl. Breed. Abs. **4**: 132.
136. ————. 1935. The genetics and cytology of certain cereals. VII. Jap. Jour. Bot. **7**: 453–469.
137. ————. 1939. Cytogenetical studies in *Avena*. III. Experimentally produced eu- and hyperhexaploid aberrants in oats. Cytologia **10**: 101–104.
138. Oehler, E. 1930. Speltoid- und Fatuoidmutationen. Züchter **2**: 93–101.
139. Oescu, C. V. 1938. Sur un cas de fausse folle-avoine homozygote dans une lignée d'*Avena sativa* L. Bull. Sect. Sci. Acad. Roumania **19**: 148–152.
140. O'Mara, J. G. 1940. Cytogenetic studies on Triticale. I. A method for determining the effects of individual *Secale* chromosomes on *Triticum*. Genetics **25**: 401–408.
141. Parker, J. H. 1922. A genetic study of aberrant and false types in Kanota oats. Rep. Kan. Agr. Exp. Sta. **1922–24**: 38–41.
142. Percival, J. 1921. The wheat plant.
143. Philiptschenko, J. 1929. Ein neuer Fall von Speltoidmutationen beim Weizen. Zeit. Ind. Abs. Ver. **52**: 406–413.
144. Philp, J. 1938. Aberrant leaf width in polyploid oats. Jour. Genet. **36**: 405–429.
145. ————. 1933. The genetics and cytology of some interspecific hybrids of *Avena*. Jour. Genet. **27**: 133–180.
146. ————. 1935. Aberrant albinism in polyploid oats. Jour. Genet. **30**: 267–302.

147. Phipps, I. F. and Guerney, H. C. 1932. A preliminary note on the origin of a B-type speltoid in *Triticum vulgare*. Austral. Jour. Exp. Biol. & Med. Sci. **10**: 215–218.
148. Pridham, J. T. 1916. Oat breeding experiments. Agr. Gaz. New So. Wales **27**: 457–461.
149. Raum, H. and Huber, J. H. 1927. Untersuchungen über Fatuoidmutationen bei Hafer. Zeit. Ind. Abs. Ver. **44**: 272–282.
150. Ru, Shou-Keng 1933. Inheritance of fatuoid characters in *Avena*. Thesis, Cornell Univ.
151. Sakamura, T. 1918. Kurze Mitteilung über die Chromosomenzahlen und die Verwandtschaftsverhältnisse der *Triticum*-Arten. Bot. Mag. (Tokyo) **32**: 151–154.
152. Sander, H. G. F. 1939. Chromosome mutations in *Avena*. Ph.D. Thesis, McGill Univ.
153. Sapehin, A. A. 1934. X-ray mutations as a source of new varieties of agricultural plants. Priroda **9**: 28–31; Pl. Breed. Abs. **5**: 94.
154. Sax, K. 1918. The behavior of the chromosomes in fertilization. Genetics **3**: 309–327.
155. ———. 1921. Sterility in wheat hybrids. I. Sterility relationships and endosperm development. Genetics **6**: 399–416.
156. Schiemann, E. 1932. Entstehung der Kulturpflanzen. Vererbungswiss. Vol. 3.
157. Schribaux, E. 1925. Hybridation naturelle chez l'avoine. Comp. Rend. Acad. Agr. France **11**: 962–963.
158. Schulz, A. 1913. Die Geschichte des Saathafers. Jahresb. Wesfälischen Prov.-Vereins Wiss. & Kunst. **41**: 204–217.
159. Schwarnikow, P. K. 1937. Über die Erhöhung der Mutationsrate bei Weizen nach langer Aufbewahrung der Samen. Genetica **19**: 188–199.
160. Sears, E. R. 1939. Amphidiploids in the Triticinae induced by colchicine. Jour. Heredity **30**: 38–43.
161. ———. 1941a. Amphidiploids in the seven-chromosome Triticinae. Univ. Mo. Agr. Exp. Sta., Res. Bull. 336.
162. ———. 1941b. Chromosome pairing and fertility in hybrids and amphidiploids in the Triticinae. Univ. Mo. Agr. Exp. Sta., Res. Bull. 337.
163. Sirodot, M. 1928. Avoines fatuoides et fatuo-steriloides. Ann. Sci. Agron. France et Etrang. **45**: 42–47.
164. Smith, S. G. 1936. Cyto-genetic studies of compactoid and speltoid mutations in *Triticum vulgare* Host. M.Sc. Thesis, McGill Univ.
165. ———. 1938. The cytogenetics of compactoid and speltoid mutations in *Triticum vulgare*. Ph.D. Thesis, McGill Univ.
166. Stadler, L. J. 1932. On the genetic nature of induced mutations in plants. Proc. 6th Int. Cong. Genet. Vol. 1: 274–294.
167. Stanton, T. R. and Coffman, F. A. 1929. Yellow-kerneled fatuoid oats. Jour. Hered. **20**: 67–70.
168. ——— *et al.* 1926. Fatuoid or false wild forms in Fulghum and other oat varieties. Jour. Hered. **17**: 152–226.
169. Surface, F. M. 1916a. On the inheritance of certain glume characters in the cross *Avena fatua* × *A. sativa* var. Kherson. Proc. Nat. Acad. Sci. **2**: 478–484.
170. ———. 1916b. Studies in oat breeding. III. On the inheritance of certain glume characters in the cross *Avena fatua* × *A. sativa* var. Kherson. Genetics **1**: 252–286.
171. Taborda de Morais, A. 1936. Estudos nas Aveias. I. As aveias portuguesas da Secção Euavena Griseb. Bol. Soc. Broteriana **11**: 49–86.
172. ———. 1937a. Les hybrides naturels d'*Avena sativa* L. Bol. Soc. Broteriana **12**: 253–286.

173. ————. 1937b. Brève discussion sur la génétique des Avoines. Bol. Soc. Broteriana **12**: 287–295.
174. ————. 1939. Estudos nas Aveias portuguesas da secção Euavena Griseb. Bol. Soc. Broteriana **13**: 573–709.
175. THELLUNG, A. 1911. Über die Abstammung, der systematischen Wert und die Kulturgeschichte der Saathaferarten. Vierteljahrschr. Naturf. Ges. Zürich **56**: 293–350.
176. ————. 1918a. Neuere Wege und Ziehle der botanischen Systematik erläutert am Beispiele unserer Getreidearten. Mitt. Naturwiss. Ges. Winterthur **12**: 109–152.
177. ————. 1918b. Neuere Wege und Ziehle der botanischen Systematik erläutert am Beispiele unserer Getreidearten. Naturwiss. Wochenschrift **33** (N.F. 17): 449–458, 465–474.
178. ————. 1928. Die Übergangsformen vom Wildhafer-Typus (*Avena agrestes*) zum Saathafer-Typus (*Avena sativae*). Rec. Trav. Bot. Néerl. **25a**: 416–444.
179. THOMPSON, W. P. AND ROBERTSON, H. T. 1930. Cytological irregularities in hybrids between species of wheat with the same chromosome number. Cytologia **1**: 252–262.
180. ———— *et al.* 1943. The artificial synthesis of a 42-chromosome species resembling common wheat. Canad. Jour. Res. C **21**: 134–144.
181. ————AND HARDING, J. 1942. Further studies on a synthetic 42-chromosome wheat. Trans. Roy. Soc. Canad. **36**: 159.
182. TRABUT, L. 1909. Contribution à l'étude de l'origine des Avoines cultivées. Comp. Rend. Acad. Sci. Paris **149**: 227–229.
183. ————. 1910. Contribution à l'étude de l'origine des Avoines cultivées. Bull. Soc. Hist. Nat. Afr. Nord **2**: 150–161.
184. ————. 1914. Origin of cultivated oats. Jour. Hered. **5**: 74–85.
185. TSCHERMAK, E. I. 1911. Über die Vererbung der Blütezeit bei Erbsen. Verh. Naturf. Ver. Brünn **49** (Abh.): 169–191.
186. ————. 1913. Über seltene Getreidebastarde. Beiträge Pflanzenzucht **3**: 49–61.
187. ————. 1914a. Die Verwertung der Bastardierung für phylogenetische Fragen in der Getreidegruppe. Zeit. Pflanzenzücht. **2**: 291–312.
188. ————. 1914b. Über die Vererbungsweise von Art-und Gattungebastarden innerhalb der Getreidegruppe. Mitt. Landw. Lehrkanzel K.K. Hochschule Bodenkultur. Wien. **2**: 763–772.
189. ————. 1918. Beobachtungen bei Bastardierung zwischen Kulturhafer und Wildhafer (*Avena fatua*). Zeit. Pflanzenzücht **6**: 207–209.
190. ————. 1929a. Kultur-und Wildhaferbastarde und ihre Beziehungen zu den sogenannten Fatuoiden. Zeit. Ind. Abs. Ver. **51**: 450–481.
191. ————. Über seltene Weizen-und Haferbastarde und Versuche ihrer praktischen Verwertung. Beiträge Pflanzenzücht **10**: 74–93.
192. UCHIKAWA, I. 1934. Genetische-cytologische Studien an Weizenspeltoiden. I. Speltoide der C. serie. Bot. & Zool. **2**: 851–864.
193. ————. 1936. Cytogenetic studies on speltoid wheat. Jap. Jour. Genet. **12**: 53–56.
194. ————. 1937. Cytogenetic studies on compactoid wheat. Jap. Jour. Genet. **13**: 9–15.
195. ————. 1938. Cytogenetic studies on short-normal type and dwarf-compactum type in compactoid wheat. Jap. Jour. Genet. **14**: 264–267.
196. ————. 1939. Cytogenetic studies on dwarf-compactoid wheat with 42-chromosomes. Jap. Jour. Genet. **15**: 315–317.
197. ————. 1941. Genetic and cytological studies of speltoid wheat. II. Origin of speltoid wheat. Mem. Coll. Agr. Kyoto Imp. Univ. **50**: 1–62.

198. Vasiliev, B. 1929. On the cytology of speltoids. Bull. Bur. Genet. (Leningrad) **7**: 31–38.
199. ———— and Kamenik, J. 1933. On the genetics of speltoids. Bull. Inst. Genetics (Leningrad) **10**: 7–17.
200. Vavilov, N. I. 1926. Studies on the origin of cultivated plants. Bull. Appl. Bot., Genet. & Pl. Breed. **16**(2): 1–248.
201. Vestergaard, H. A. B. 1921. Beobachtungen vom Zuchtgarten. Zeit. Pflanzenzucht. **8**: 192–195.
202. Watkins, A. E. 1927a. Genetic and cytological studies in wheat. III. Jour. Genet. **18**: 375–396.
203. ————. 1927b. Genetic and cytological studies in wheat. IV. Jour. Genet. **19**: 81–96.
204. ————. 1928. The genetics of wheat species crosses. I. Jour. Genet. **20**: 1–27.
205. ————. 1930. The wheat species: A critique. Jour. Genet. **23**: 173–263.
206. ————. 1940. The inheritance of glume shape in *Triticum*. Jour. Genet. **39**: 249–264.
207. ———— and Cory, F. M. 1931. Genetic and cytological studies in wheat. V. Jour. Genet. **25**: 55–90.
208. ———— and Ellerton, S. 1940. Variation and genetics of the awn in *Triticum*. Jour. Genet. **40**: 243–270.
209. Winge, Ø. 1917. The chromosomes, their number and general importance. Comp. Rend. Lab. Carlsberg **13**: 131–275.
210. ————. 1924. Zytologische Untersuchungen über speltoide und andere mutantenähnliche Aberranten beim Weizen. Hereditas 5: 241–286.
211. Zade, A. 1912a. Der Flughafer (*Avena fatua*). Arb. Deut. Landw. Ges. Heft. 229.
212. ————. 1912b. Die Zwischenformen vom Flughafer (*Avena fatua*) und Kulturhafer (*Avena sativa*). Fühlings Landw. Zeit. **61**: 369–384.
213. ————. 1918. Der Hafer.
214. Zhegalov, S. I. 1920. On the genetics of oats. All Russ. Cong. Pl. Breed., Saratov, Rep. Vol. 3: 80–86.
215. Zirkle, C. 1935. The beginnings of plant hybridization.

for CONVENIENCE...

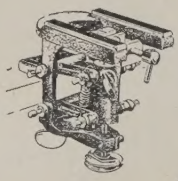


In Sectioning Biological Specimens

Biologists, instructors, and students alike find it easy to cut sections accurately with these Spencer Microtomes:

No. 810 ROTARY MICROTOME (above) — an instrument with automatic feed mechanism for rapid, uniform serial sectioning.

No. 900 TABLE MICROTOME— a low priced model for cutting uniform sections by hand.



For complete information, write dept. K93.

American Optical
COMPANY
Scientific Instrument Division
Buffalo 15, New York

Manufacturers of the **SPENCER** *Scientific Instruments*

Future Contents of
THE BOTANICAL REVIEW

Articles received and awaiting publication

Cytology and Genetics of Forage Grasses	W. M. MYERS *U. S. Bureau of Plant Industry*
Anthocyanin Pigments of Plants	F. BLANK *Swiss Federal Institute of Technology*
Osmosis and the Movement of Water in Plants ..	T. C. BROYER *University of California*
Destructive Foreign Plant Diseases not known to be established in North America	N. REX HUNT *Bureau of Entomology and Plant Quarantine*
Rubber Formation in Plants	JAMES BONNER and A. W. GALSTON *California Institute of Technology*
Ecology of Marine Algae	V. J. CHAPMAN *Cambridge University*
The Endosperm in Seed Development	R. A. BRINK and D. C. COOPER *University of Wisconsin*
Antibiotic Products of Fungi	D. F. HOLTMAN *University of Tennessee*
Absorption of Electrolytes in Large Plant Cells. II	W. J. V. OSTERHOUT *Rockefeller Institute for Medical Research*
Recent Work on Minor Elements and Crop Growth. II	WINIFRED E. BRENCHLEY *Rothamsted Experimental Station*
Plant Tissue Cultures. II	PHILIP R. WHITE *Rockefeller Institute for Medical Research*
Cytoplasmic Inclusions of the Plant-Like Flagellates. II	R. P. HALL *New York University*
Recent Developments in Fungicides—Spray Materials. II	JOHN W. ROBERTS *U. S. Department of Agriculture*
The Oedogoniaceae. II	LEWIS HANFORD TIFFANY *Northwestern University*
The Chemistry and Physiology of the Pectins. II	JAMES BONNER *California Institute of Technology*
The Relation of Weather to Fungus Diseases of Plants. II	C. E. FOISTER *Department of Agriculture for Scotland*
The Angiosperm Embryo Sac	P. MAHESHWARI *Dacca University*
Plant Diseases During the Years 1941–1945 in the United States and Canada	N. E. STEVENS *University of Illinois* and R. B. STEVENS *University of Louisville*
Plant Disease Control by Unusual Methods	N. E. STEVENS and INEZ NIENOW *University of Illinois*